A DIAPSID REPTILE
FROM THE
PENNSYLVANIAN OF KANSAS

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This is the first of a series of Special Publications honoring the contributions of Dr. Theodore H. Eaton to the fields of vertebrate paleontology and zoology. The series will center around the Pennsylvanian fauna of eastern Kansas, and will include papers on fishes, amphibians and reptiles, as befits the wide-ranging interests Dr. Eaton has shown in his research.

E. O. WILEY
LARRY D. MARTIN
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LAWRENCE, KANSAS

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INTRODUCTION

All living reptiles can be grouped into four orders: Chelonia, Rhynchocephalia, Squamata and Crocodilia. The latter three can be associated with the largest assemblage of fossil reptiles, collectively called diapsid reptiles. The diapsid condition refers to the presence of two pairs of temporal openings on the skull roof behind the orbits. This condition has been retained in a primitive form in crocodilians and in the sole living rhynchocephalian *Sphenodon punctatum* but has been modified in the squamates by the progressive loss of dermal bones in the temporal region.

Diapsid reptiles have an evolutionary history long thought to extend only into the late Permian. The early evolution of this assemblage is not well documented in the fossil record. Consequently, the origins and phyletic relationships of member groups have been subject to dispute.

On several occasions, Watson (1951, 1954) reiterated his belief in Goodrich's concept of a basic dichotomy among reptiles. According to this theory, one group called the Theropsida led to mammals and included the mammal-like reptile orders Pelycosauria and Therapsida. The other group, the Sauropsida, also called "true" reptiles, included the diapsid reptiles and the turtles (Chelonia). Watson argued for independent origins of the Theropsida and Sauropsida from anthracosaurian amphibians via some unknown intermediate forms. He based this conclusion on his theory of the evolution of the ear (Watson, 1953). He discounted the possibility of captorhinomorphs having given rise to the Sauropsida and, hence, to the diapsid reptiles. He actually placed the Captorhinomorpha among the Theropsida. In 1957 Watson suggested that the diapsids evolved from seymoriamorph anthracosaurs via the Millerosauria.

Vaughn (1955) also accepted the sauropsid-theropsid dichotomy and felt that the Sauropsida, and therefore diapsids, could not be derived from captorhinomorphs.

Romer (1966) rejected Watson's theory of the evolution of the ear and reiterated his belief that all true reptiles can be derived from primitive captorhinomorphs. In a review of early reptilian evolution, Romer (1967) suggested not only that the sauropsid-theropsid dichotomy, insofar as it exists, has little phylogenetic significance, but also that the term Sauropsida has no systematic or phylogenetic meaning. Furthermore, he emphasized that the diapsids may not belong to a single phyletic unit. He argued that two discrete diapsid groups should be recognized, the Archosauria and the Lepidosauria. He proposed that the Lepidosauria (the squamates, rhynchocephalians and the ancestral eosuchians) on the one hand, and the Archosauria (the two dinosaur orders, pterosaurs, crocodilians and the basic Triassic group, the thecodonts) on the other, evolved separately from the ancestral captorhinomorphs. It was his suggestion that the milleretid skull pattern represents an intermediate stage between the ancestral captorhinomorphs and the lepidosaurs.

In 1967 Reig set forth, and later (1970) elaborated, a radically different hypothesis for the origin of archosaurs. He proposed that the ancestors of archosaurs should be sought among varanopsid pelycosaurs. Most of the comparable features cited by Reig as indicative of phylogenetic relationships are, however, primitive characteristics found in the ancestral captorhinomorphs (Romer, 1971).

Gow (1972), in his reconsideration of the milleretids, contended that this group gave rise directly to the Squamata. He felt on the other hand, that the Rhynchocephalia and the Archosauria had an entirely independent origin.

The above workers have based their theories of the origins and early evolution of the

diapsid reptiles mainly on the meager evidence provided by the known Permian cotylosaurs and on the Upper Permian and Triassic diapsids. Thanks mainly to the labors of Robert L. Carroll and the late Frank E. Peabody, the problem of the origins and early evolution of diapsid reptiles can be reconsidered. Carroll, during a period of about ten years, described and reconsidered all of the available Pennsylvanian and Lower Permian specimens of primitive captorhinomorphs. One significant conclusion became evident: the described members of this group conform to a single conservative morphological pattern and remained sufficiently generalized to indicate that primitive captorhinomorphs could be ancestral to most subsequent reptilian lineages (Carroll and Baird, 1972; Clark and Carroll, 1973).

In 1952, Peabody published a partial description of *Petrolacosaurus kansensis* and suggested that this reptile from the Upper Pennsylvanian was a member of the most primitive diapsid order, the "Eosuchia." The fragmentary nature of the specimens available for this study led others, however, to question Peabody's contention. Subsequently Peabody spent two grueling summers—1953 and 1954 —collecting more specimens but died before he could undertake a reconsideration of the anatomy of *Petrolacosaurus*. This collection forms the basis of the present study. These specimens show that *Petrolacosaurus* is a diapsid reptile with affinities to both primitive captorhinomorphs and the earliest "eosuchians."

My interest in *Petrolacosaurus* was aroused during a visit to the Kansas University Museum of Natural History in Lawrence, Kansas, where T. H. Eaton invited me to examine this interesting reptile. It became apparent that the available specimens of this genus, much superior to those described in 1952, warranted a thorough reconsideration. The purpose of the present study, undertaken with Dr. Eaton's kind permission, is to describe the earliest known diapsid reptile, *Petrolacosaurus kansensis*, and to consider its relationship to both

primitive captorhinomorphs and to more advanced diapsid reptiles. The problem of hearing in *Petrolacosaurus* and other early reptiles forms an integral part of this study.

DESCRIPTIVE AND SYSTEMATIC HISTORY

Lane first described *Petrolacosaurus kansensis* in 1945 and referred the genus to the family Sphenacodontidae of the order Pelycosauria (1946) on the basis of a tarsus found with an isolated hindlimb and pelvis. An isolated forelimb and some other skeletal remains were described as *Podargosaurus hibbardi* and referred to the family Araeoscelidae of the order Protorosauria (1946) on the basis of the slender humerus, radius, ulna, and the ribs.

In 1952 Peabody published a detailed description of the Garnett reptile and placed *Podargosaurus* in synonymy with *Petrolaco-*

saurus. He concluded that "*Petrolacosaurus* represents a new family of primitive reptiles showing relationships which place it at the base of the Eosuchia while also evidencing strong relationship with primitive cotylosaurs." The fragmentary nature and immaturity of the known specimens led others to reject his conclusions. Peabody's association of an isolated edaphosaurian pelvis (KUVP 1425) with the *Petrolacosaurus* material added to the confusion.

Watson (1954), after an examination of the known specimens concluded that this genus was a theropsid. He based his conclusion on the nature of the quadrate in the small, immature skull. He felt that this quadrate was similar to those in pelycosaurs and captorhinomorphs.

Although he reserved final judgment until a more complete description was undertaken, Vaughn (1955) was inclined to agree with Watson's diagnosis. He also suggested that *Petrolacosaurus* may be related to *Araeoscelis* and that the former genus may become the type of a new family of Araeoscelidia.

Tatarinov (1964) reassigned the Family Petrolacosauridae to the Order Araeoscelidia; he based his conclusions on the similarities seen in the palate and postcranial skeleton of *Petrolacosaurus* and *Araeoscelis*. Tatarinov followed Romer (1956), however, in placing the Araeoscelidia within the Subclass Euryapsida.

Romer (1956) tentatively placed *Petrolacosaurus* within the Family Ophiacodontidae (Pelycosauria). In 1966 in a joint paper with Stovall and Price, Romer maintained that "Apart from the possible but unproven diapsid nature of the temporal region, there is no reason to assign *Petrolacosaurus* to the Eosuchia." He felt, however, that certain diagnostic features in the post-cranial skeleton ". . . strongly indicate that this genus belongs to a group of archaic edaphosaurians from which both *Edaphosaurus* and, at a much later time, the caseids may have arisen."

SYSTEMATIC DESCRIPTION

Family PETROLACOSAURIDAE Peabody, 1952[1]

Genus *Petrolacosaurus* Lane, 1945

Type species.—*Petrolacosaurus kansensis* Lane, 1945.

Synonym.—*Podargosaurus* Lane, 1945.

Occurrence.—Upper Pennsylvanian of Kansas.

Diagnosis.—Same as for species.

Petrolacosaurus kansensis Lane, 1945
Figs. 1-25

Synonym.—*Podargosaurus hibbardi* Lane, 1945.

Revised diagnosis.—Medium sized early diapsid reptile (Fig. 1) with well developed superior and inferior temporal fenestrae and elongate, narrow suborbital fenestra. Parietal without the ventrolateral flange that extends into the superior temporal fenestra in younger diapsids; posterior splenial bone present in mandible; marginal dentition unusually thin-walled. Six elongate cervical vertebrae; twenty six presacral vertebrae; a pair of mammillary processes on the neural spine of first sacral vertebra; large dorsal isciadic notch; slender forelimbs equal in length to more massive hindlimbs; propodials equal in length to epipodials.

Distinguished from captorhinomorph reptiles by relatively smaller skull, superior, inferior temporal fenestrae and suborbital fenestra, greater length of neck, partial rather than complete coossification of atlantal centrum and axial intercentrum, mammillary

processes on neural spines and excavation of neural arches of dorsal vertebrae, longer tail, and greater relative length and slenderness of limbs.

Separated from *Araeoscelis* by the inferior temporal fenestra, more lightly built skull and dentition and straight ventral margin of cheeks.

Differs from other diapsid reptiles by simple lateral embayment of parietal rather than a ventrolateral flange in addition to the embayment, larger lacrimal and squamosal, larger quadratojugal, lack of retroarticular process, denticulate parasphenoid and massive stapes.

Holotype.—KUVP (Kansas University Museum of Natural History) 1424, adult right hindlimb consisting of most of the femur, the distal part of the tibia and fibula in articulation with a complete pes.

Hypodigm.—KUVP 1423, complete right forelimb, immature. KUVP 1426, right hindlimb lacking femur, immature. KUVP 1427, splenial, vertebral column, scattered ribs, forelimbs, partial pectoral girdle, partial hindlimb, immature. KUVP 1428, questionable skull fragment, partial maxilla, partial vertebral column, scattered ribs, incomplete forelimbs and hindlimbs, partial pelvic girdle, scattered gastralia, immature. KUVP 1429, left forelimb, immature. KUVP 8351, partial skull, five cervical vertebrae, immature. KUVP 8355, right carpus, immature. KUVP 9950, isolated right parietal, mature. KUVP 9951, partial skull, vertebral column, ribs; on separate blocks femora and pelves, left lower hindlimb, right lower hindlimb, slightly immature. KUVP 9952, partial skull (mainly dermal skull roof), mature. KUVP 9956, a series of articulated vertebrae from C3 to S2, with some closely associated ribs, a short series of articulated caudal vertebrae, mature. KUVP 9957, three separate blocks containing left scapulacoracoid with humerus, radius and ulna in articulation and partial carpus, slight-

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[1] The family Petrolacosauridae has been formerly included in the order Eosuchia (Peabody, 1952; Reisz, 1977). Study of the above order indicates that it is an artificial assemblage of Late Paleozoic and Mesozoic diapsid reptiles. The "Eosuchia" has no taxonomic validity because there are no known diagnostic features that can distinguish it from other diapsid reptiles. The diagnostic features of the monogeneric family Petrolacosauridae are the same as for the genus.
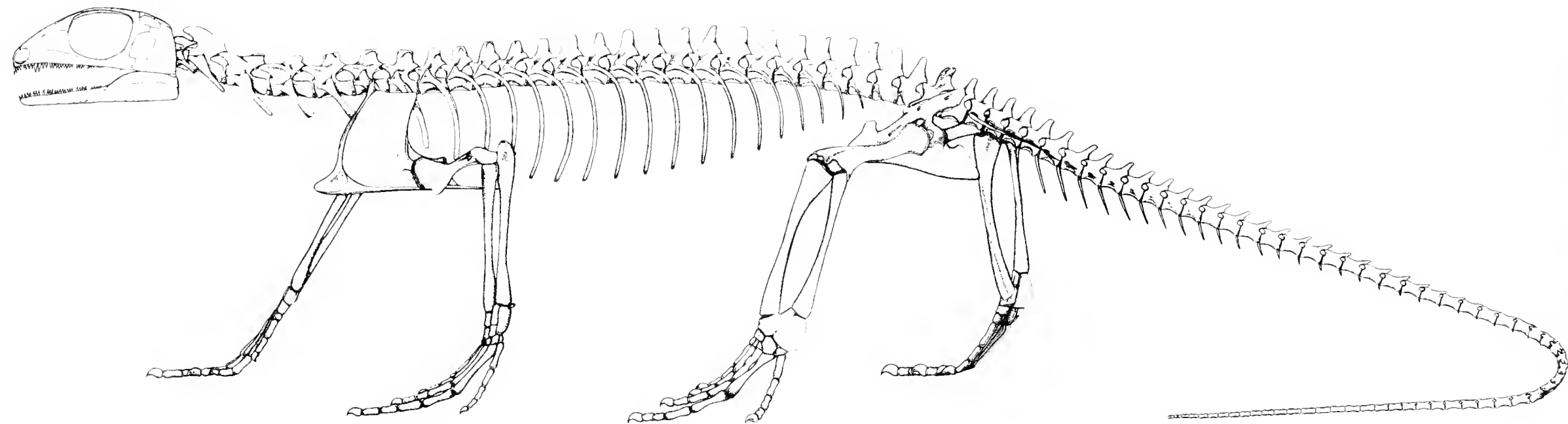
Fig. 1.—*Petrolacosaurus kansensis.* Reconstruction of skeleton, × 0.75. Composite.

ly immature. KUVP 9958, left clavicle, slightly immature. KUVP 9959, seven separate blocks containing badly preserved subadult skull, interclavicle, immature, lower jaws, scattered vertebrae and ribs, forelimbs, hindlimbs, both ilia, very immature. KUVP 9961, left pelvis, mature. KUVP 9962, ilium with first sacral rib attached, immature. KUVP 10320, badly preserved specimen containing skull fragments, vertebrae, hindlimbs, immature. KUVP 33602, isolated left maxilla, slightly immature. KUVP 33603, fragments of skull material, distal end of humerus, immature. KUVP 33604, scattered skull material, atlas-axis complex, cleithrum, distal end of humerus, radius, ulna, mature. KUVP 33605, seven posterior dorsal vertebrae and first sacral vertebra, first sacral rib, all articulated, slightly immature. KUVP 33606, partial skull, posterior dorsal, sacral and anterior caudal vertebrae, some associated ribs, clavicle, partial scapulacoracoid, humerus, partial pelvis, right hindlimb with scattered pes, mature. KUVP 33607, slightly dissociated skull, first three cervical vertebrae, cleithrum, right scapulacoracoid, olecranon, partial carpus, mature. KUVP 33608, poorly preserved skull and cervical vertebrae. KUVP 33609, right scapulacoracoid, mature.

OSTEOLOGY

Skull

By using the available material, it has been possible to obtain a composite, fairly accurate reconstruction of the skull, in which most of the external details of the dermal roof, occiput, palate, the lateral and medial aspects of the mandible can be discerned. The quality of preservation prevents any reconstructions of the braincase beyond those seen in Figs. 3b and 4.

The skull as reconstructed has the principal dimensions listed in Table 1. These measurements indicate that *Petrolacosaurus* has retained many of the primitive cranial proportions seen in primitive captorhinomorphs

but also shows a number of significant departures from this pattern.

In dorsal aspect (Fig. 3a) the skull is long and relatively narrow. The width at the quadrate exceeds, only slightly, one-half the length of the skull. Maximum width is reached just behind the orbits in the region of the temporal openings. In the antorbital region the skull table extends far laterally, obscuring the posterior part of the narial opening and the maxilla when seen in dorsal view. In the postorbital region both temporal fenestrae are visible from above. The summit of the skull (in cross-sectional view) in this area is at the level of the medial suture of the postfrontal wedge. Laterally the skull roof slopes gently down to the level of the upper temporal fenestra. From here the grade of the downward slope increases greatly. The curvature between the skull table and the cheek in the temporal region is thus formed by the ventral part of the postfrontal that lies beneath the postorbital and the dorsal part of the postorbital and squamosal. The posterior margin of the skull table is deeply emarginated where the dorsal aspect of the parietal ends.

The antero-posterior slope of the skull table is illustrated in Fig. 2a. The skull is long and shallow in lateral view. The maximum height, reached in the orbital region represents only about 35 per cent of the length of the skull. The gently convex posterior margin of the skull is nearly perpendicular to the ventral margin. The jaw articulation lies only slightly below the level of the tooth row. The marginal tooth row occupies 58 per cent of the skull length.

The outline of the palate is defined by the ventral edges of the cheeks and by the posterior margin of the braincase (Fig. 3b). The internal nares, bounded by the premaxilla, maxilla, palatine and vomer, are long and narrow. Both the vomer and palatine extend ventrally at the margin of the opening forming ridges. The interpterygoid vacuities are of moderate size. The suborbital fenestrae are well developed, elongate openings, albeit smaller than in *Youngina* (Olson, 1936; Gow,
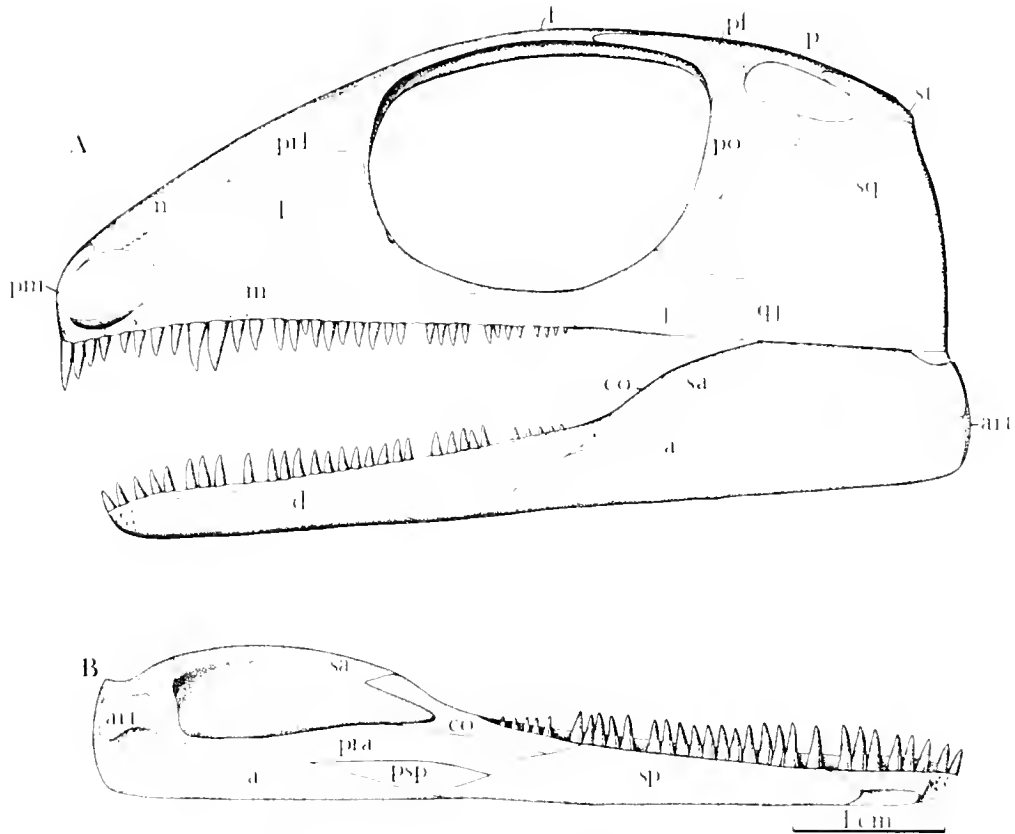
FIG. 2.—*Petrolacosaurus kansensis* Lane. Reconstruction of skull and mandible in lateral view (A), and of mandible in medial view (B) based mainly on specimens KUVP 9952 and KUVP 33607, × 2. Abbreviations used in Figs. 2-13: a, angular; ac, atlantal centrum; an, atlantal neural arch; art, articular; ax, axial centrum; axi, axial intercentrum; bo, basioccipital; bs, basisphenoid; bt, basipterygoid process; co, coronoid; ct, cultriform process; d, dentary; ec, ectopterygoid; ex, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; o, opisthotic; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal; pra, prearticular; prf, prefrontal; pro, prootic; ps, parasphenoid; psp, postsplenial; pt, pterygoid; q, quadrate; qf, quadrate foramen; qj, quadratojugal; r1, atlantal rib; r2, axial rib; s, stapes; sa, surangular; sc, sclerotic plates; sm, septomaxilla; so, supraoccipital; sq, squamosal; st, supratemporal; t, tabular; tr. fl. pt, transverse flange of pterygoid; v, vomer.

1975). With the exception of the ectopterygoid, the paired palatal bones bear denticles; in addition, three major rows of large teeth radiate laterally, diagonally, and anteriorly from the basicranial articulation. Small denticles are also present on the parasphenoid. The palate is anchored directly to the dermal skull roof at three points: anteriorly to the premaxilla and laterally to the maxilla and to the jugal. Posteriorly, the palate is indirectly anchored to the skull roof by the quadrate and the braincase. The occipital condyle is set only slightly anterior to the posterior margin of the jaw articulation. The subtemporal fossae are quite large, occupying about 23 per cent of the palatal area.

The overall impression from the occipital aspect (Fig. 4) is of a fairly low, wide skull. Part of the skull roof is visible in this view. A well developed nuchal ridge extends from the dorsal occipital border to the foramen magnum, which has the same height as width. The post-temporal fenestrae are large. The occipital condyle is located low on the occipital face, only 4 mm from the line joining the ventral borders of the quadratojugals and
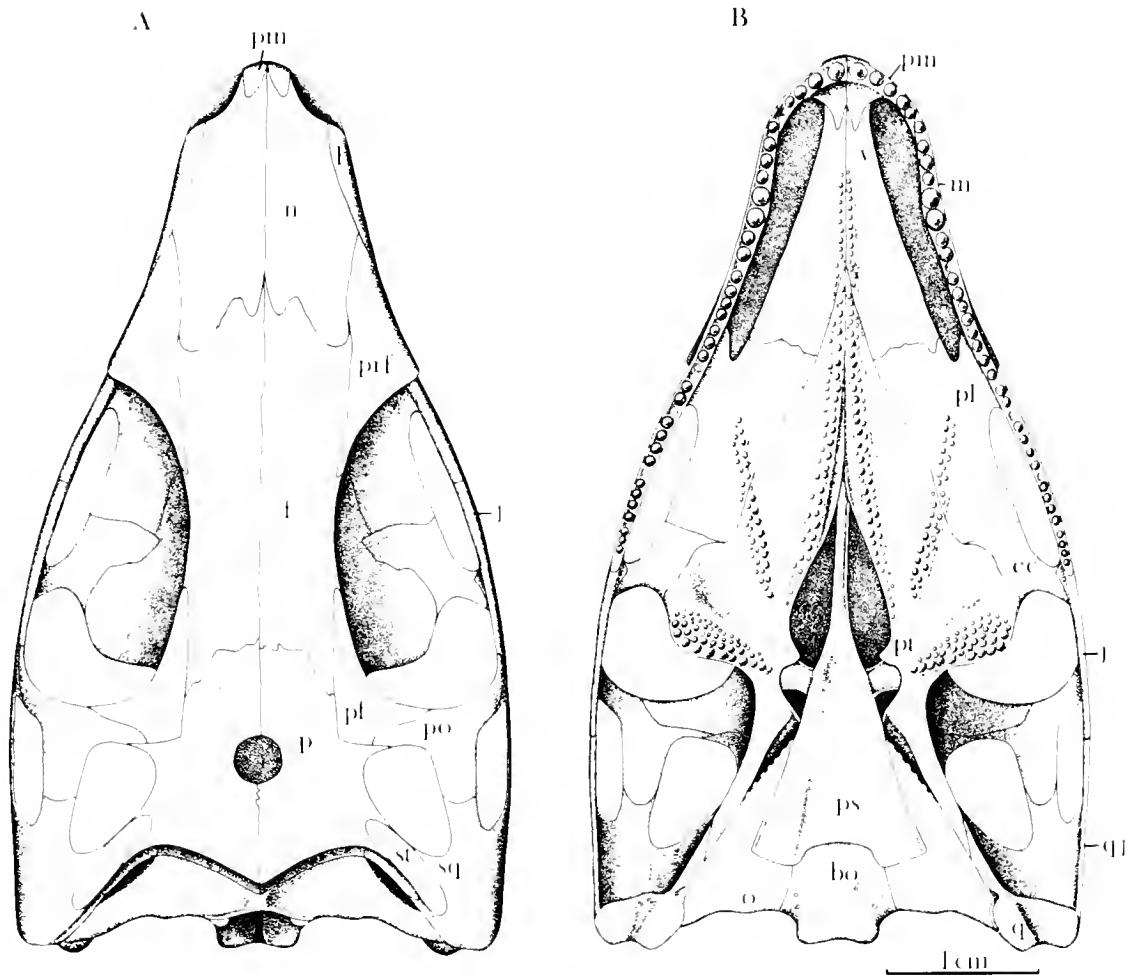
FIG. 3.—*Petrolacosaurus kansensis* Lane. Reconstruction of skull in dorsal (A), and ventral (B) views, based mainly on specimens KUVP 9952, 33606 and 33607, × 2. See Fig. 2 for key to abbreviations.

about 13 mm below the posterior edge of the parietal.

The largest openings in the skulls are the orbits. Each occupies 38 per cent of the total skull length. The orbits incise the skull table deeply.

The upper temporal fenestra faces mainly dorsally, but is also visible in lateral view because of the curvature of the circumtemporal bones. The lower temporal fenestra, on the other hand, faces mostly laterally, but is also visible from the dorsal aspect. Its posteroventral corner is not preserved. The postorbital bar, composed of parts of the postorbital bar, composed of parts of the post-

frontal, postorbital, and jugal is slender; the orbit and temporal fenestra are, therefore, not widely separated.

The external naris is relatively large in relation to the skull. This opening faces anterolaterally and only slightly dorsally. The external naris is floored laterally by a shelf formed by the premaxilla and maxilla.

A large pineal foramen opens dorsally on the midline, approximately at the level of the anterior margin of the upper temporal fenestra.

The lower jaw, as reconstructed (Fig. 2), has the principal dimensions listed in Table 1.
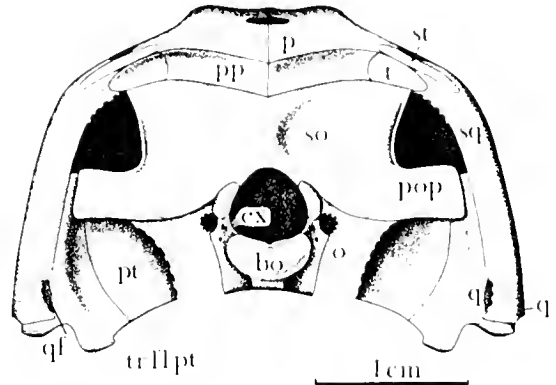
Fig. 4.—*Petrolacosaurus kansensis* Lane. Reconstruction of skull in occipital view, mainly based on specimens KUVP 9951 and 33607, ×2. See Fig. 2 for key to abbreviations.

TABLE 1.—Measurements of the skull and lower jaw of *Petrolacosaurus kansensis*, made primarily on the basis of the restoration of KUVP 33607. Measurements of the eaptorhinomorph *Protorothyris archeri* are based mainly on the type specimen (Clark and Carroll, 1973). Measurements in millimeters.

	Petrolacosaurus kansensis	Protorothyris archeri (MCZ 1532)
Length of skull	59	56
Width of skull in the temporal region	33	31
Height of skull at the orbit	20	20
Length of tooth row	33	37
Length of orbit	22	16
Antorbital length	21	22
Temporal length°	13	17
Length of internal naris	17	15
Length of suborbital fenestra	11	
Length of subtemporal fossa	20	20
Length of lower jaw	57	54
Length of tooth row on lower jaw	30	34
Height of lower jaw	10	10
Length of adductor fossa	16	15
Height of adductor fossa	5	7

° Temporal length is measured from the posterior end of the supratemporal to the orbit.

It is a long, slenderly built structure, very narrow in height and width. The tooth row occupies 53 per cent of the length of the mandible. The coronoid area is gently convex, expanding dorsally well above the level of the alveolar shelf. Posteriorly the dorsal border curves slightly ventrally to the level of the articular. There is no retroarticular process. The ventral border of the ramus is nearly straight. The adductor fossa is long, occupying 30 per cent of the length of the mandible. Between its anterior, strongly acute angle (formed by the coronoid) and its wide, gently concave posterior end (formed by the articular) the fossa expands posteriorly between the prearticular and surangular. The foramen intermandibularis caudalis is not evident, but this may be due to partial disarticulation of the adjacent bones in the mandible.

With the possible exception of the maxilla, lacrimal and quadratojugal, all the bones of the dermal skull roof are sculptured. The bones are marked by slight anastamosing grooves and ridges that radiate from the center of ossification. On the cheek bones sculpturing is restricted to the area immediately surrounding the centers of ossification. The roofing bones, on the other hand, are almost completly covered by sculpturing. In a number of specimens sculpturing appears to be more extensive than on others. Preparation of the inner surface of these skulls reveals that some sculpturing is apparent even on the ventral aspect of the bones. Possibly, in these specimens, crushing was so severe that the

normal sculpturing was exaggerated by the superposition of the internal bone structure onto the surface. On the lower jaw, only the anterior one-third of the dentary is sculptured. Near the tip the lateral surface of the dentary has delicate rounded pitting. More posteriorly the pitting takes on the shape of elongate grooves.

Exposure of the internal surface of the skull roof of *Petrolacosaurus* revealed the presence of a series of ridges or thickened areas along the major lines of cranial stresses. These ridges (Fig. 25) form a framework of strengthened areas that connect the orbital margin with the snout, maxilla and suspensorium. What makes the ridges seen in *Petrolacosaurus* significant is their relative thickness when compared to the much thinner areas of the dermal skull roof and palate. The use of the resin imbedding compound during preparation of the skulls made complete removal of the matrix possible. This revealed that in the non-ridged areas the skull is made of very thin bone. The anteromedial part of the prefrontal, the medial half of the nasal, the anteroventral portion of the squamosal and most of the quadratojugal, are less than one-tenth the thickness of the ridged areas of the same skull. Such differences in the thickness of the skull elements cannot be attributed to some unusual type of preservation because other genera, found in the same deposits do not show such variation in bone thickness. In *Captorhinus* and *Dimetrodon* (Heaton, 1979; Romer and Price, 1940), where the external and internal surfaces of the skull are known in great detail, the differences in bone thickness do not approach the range seen in *Petrolacosaurus*. The internal surfaces of the skull roof and palate in Permian and Lower Triassic "eosuchians" are inadequately known for comparative purposes.

Dermal Bones of the Skull Roof

Premaxilla.—The paired premaxillae form the anterior margin of the skull. Each element has three slender processes that connect the dorsal, lateral and palatal sides of the skull to constitute the region of the snout.

The unusually slender nasal ramus of each premaxilla, exposed in both external and internal views in KUVP 9952, join at the midline to form the anterior border of the snout. The dorsal tips appear as slight posterior projections on the dorsal surface of the skull and fit into the bifurcated anterior ends of the nasals. The dorsal process reaches its greatest width at the point where it becomes visible on the superior surface of the skull.

The maxillary ramus contributes to the ventral border of the external naris and meets the maxilla in a long diagonal suture. In dorsal view the maxillary ramus gives a rounded outline to the snout.

The palatal ramus forms a continuous shelf anteriorly that extends between the external nares; it also forms the rounded anterior border of the internal naris. At the midline the premaxilla forms a wedge-like posterior vomerine process best seen in KUVP 8351 (Fig. 5), that fits into a corresponding slot in the vomer.

Anteriorly and laterally, the premaxilla is sculptured and is pierced by small foramina. In lateral view, the generally slender appearance of the premaxilla is accentuated by the height and extreme slenderness of the dorsal process and by the emargination of the maxillary process, where a medially directed flange provides support for the nasal capsule. There are from three (KUVP 9952) to five (KUVP 33607) slender, conical premaxillary teeth on either side of the midline.

The premaxillae of the protorothyridids *Hylonomus*, *Paleothyris*, and *Protorothyris* are similar to but slightly more massive than those of *Petrolacosaurus*. Reconstructions of these protorothyridids (Carroll and Baird, 1972; Clark and Carroll, 1973) show broad butt joints between the premaxillae and vomers. This is unlikely, especially since the anterior end of the vomer in *Paleothyris* is narrow and bifurcate. The vomerine process of the premaxilla is poorly known in protorothyridids.
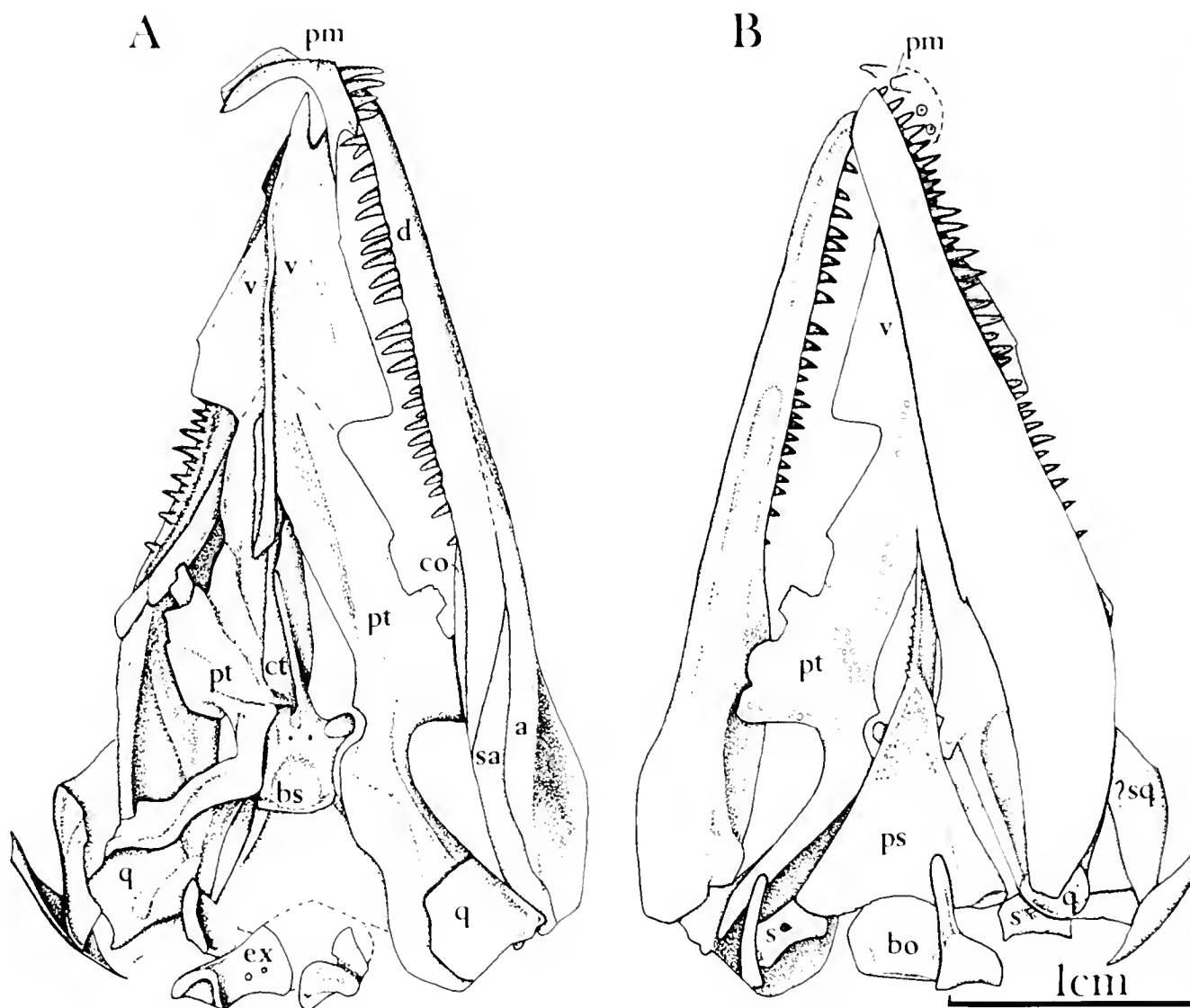
FIG. 5.—*Petrolacosaurus kansensis* Lane. Immature skull and lower jaws, KUVP 8351, × 4. (A) Dorsal view of palate exposed by loss of skull roof, oblique view of lower jaws. (B) Ventral view of palate and oblique view of lower jaws. For key to abbreviations, see Fig. 2.

Maxilla.—As in primitive captorhinomorphs and "eosuchians," the maxilla is the longest bone of the skull roof. It extends from the midpoint of the external naris past the midpoint of the orbit, over 53 per cent of the skull length. It forms the posteroventral border of the external naris but is excluded from the orbit by the lacrimal and the jugal (KUVP 9951, Fig. 6). Anteriorly, the maxilla is suturally attached to the premaxilla over a large surface area, as indicated by the rugose area on the anterior medial surface of the maxilla in KUVP 33602 (Fig. 9). Together with the premaxilla, the maxilla forms not only the ventral border of the external nares but also a medially directed shelf for the nasal capsule.

Posteriorly, the bone expands dorsally to
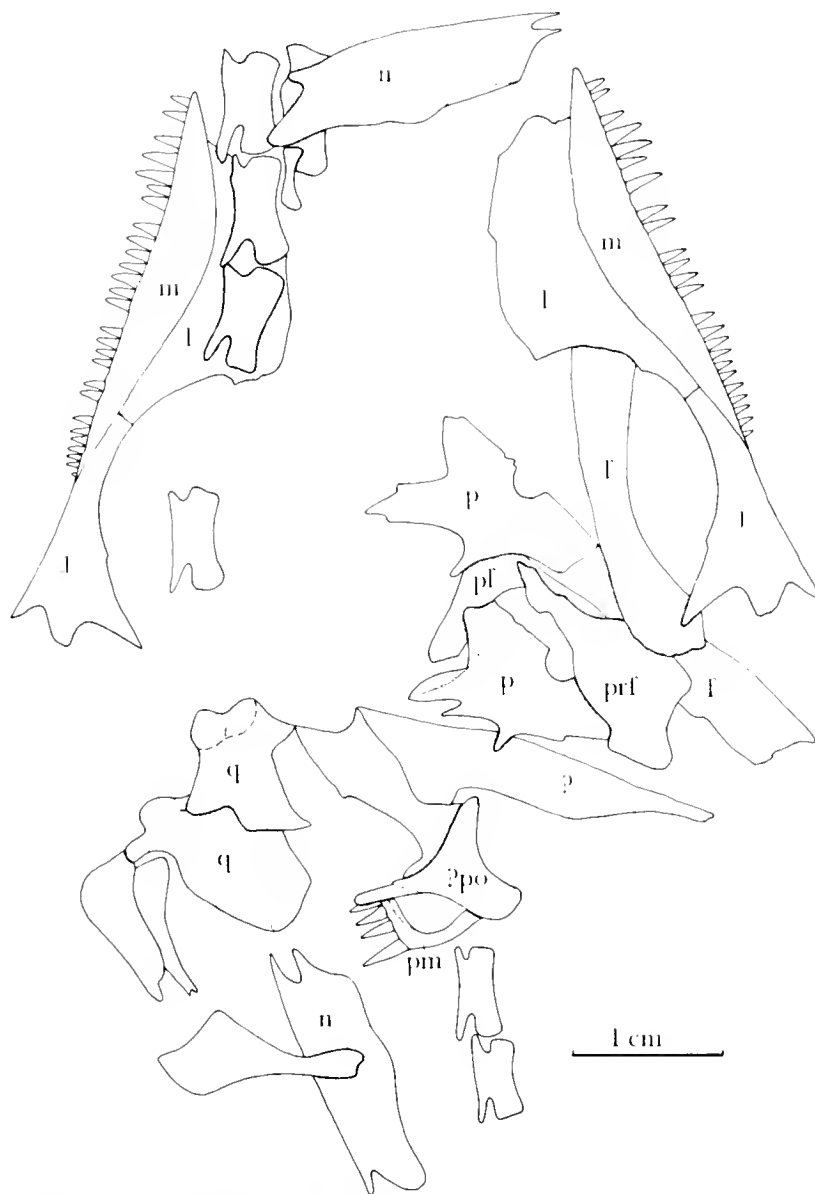
Fig. 6.—*Petrolacosaurus kansensis* Lane. Mature skull and caudal vertebrae, partially scattered, KUVP 9951, × 2. Braincase of same specimen shown in Fig. 7. See Fig. 2 for key to abbreviations.

reach its greatest vertical expansion immediately behind the level of the caniniform teeth, one-third of the distance from the anterior end of the maxilla. From this summit, the dorsal border of the maxilla slopes gently posteroventrally in an almost straight line. The lateral surface of the bone is pierced by small labial foramina, probably for cutaneous branches of the superior alveolar nerve and the maxillary artery. The lower margin is nearly straight, as in primitive captorhinomorphs and younginid "eosuchians."

The internal surface of the maxilla is more important taxonomically than the lateral. As in all primitive reptiles, the simple conical subthecodont maxillary teeth are attached to
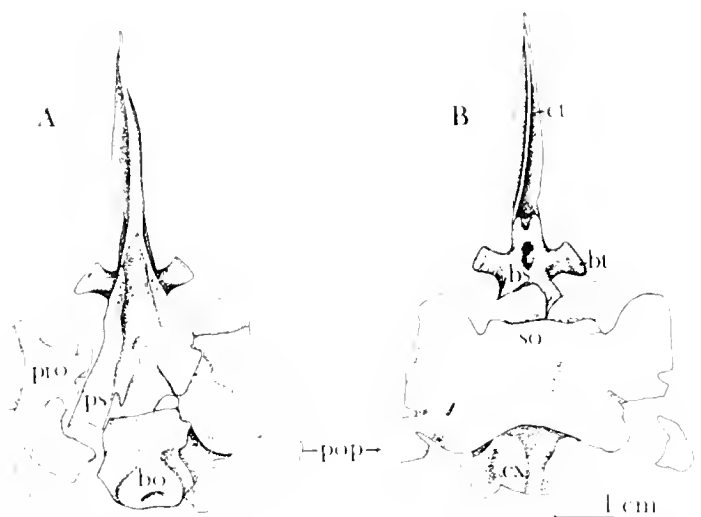
Fig. 7.—*Petrolacosaurus kansensis* Lane. Braincase of adult individual, KUVP 9951, × 2. Braincase exposed in ventral (A) and dorsal views (B), with the lateral, occipital and ventral elements compressed into a single plane. See Fig. 2 for key to abbreviations.

the alveolar shelf. In KUVP 9952, the entire left maxilla is exposed. Thirty teeth are in place, with room for five others. Laterally the teeth are covered by a thin sheet of bone that extends up to one-third of the length of the teeth below the alveolar shelf. The medial surface of the alveolar shelf is smooth in the region where it forms the lateral border of the internal naris and the lateral border of the suborbital fenestra. Between these two openings, directly beneath the anterior margin of the orbit, the alveolar shelf bears a small striated process, that is exposed in both KUVP 9952 (Fig. 8b) and KUVP 33602 (Fig. 9a). This process which occupies only 17 per cent of the length of this bone, is sutured to the palatine. It is significant that, as in all "eosuchians," the maxilla in *Petrolacosaurus* is attached directly to the palate only through this process. Posterior to this contact with the palatine, the maxilla forms the lateral border of the suborbital fenestra. The maxilla is not attached to the ectopterygoid. In primitive captorhinomorphs and pelycosaurs, on the other hand, the maxilla is sutured behind the internal naris (more than 50 per cent of the total length of the

bone) to both the palatine and the ectopterygoid.

There is no buttressing on the medial surface of the maxilla, above the caniniform teeth. This area is somewhat strengthened, however, by the ventral margin of the lacrimal which fits into a long longitudinal groove along the dorsal margin of the maxilla. The cross-section of the maxilla (Fig. 9b) in the region of the canines shows that the alveolar shelf is hollowed out from above, giving the maxilla the outline of an inverted letter "h."

Septomaxilla. — The septomaxilla, preserved only in KUVP 9952 (Fig. 8), is a thin sheet of bone whose shape and relationships cannot be determined because of crushing. It was probably attached to the anterior edge of the maxilla. In most primitive reptiles the septomaxilla, when preserved, appears as a thin rectangular sheet of bone that has been curved around a simple cone (Heaton 1979). Only in pelycosaurs is the septomaxilla robust with a thickened base and a large vertical sheet placed transversely in the posterior portion of the external naris (Romer and Price 1940).

Lacrimal.—The lacrimal in KUVP 33607
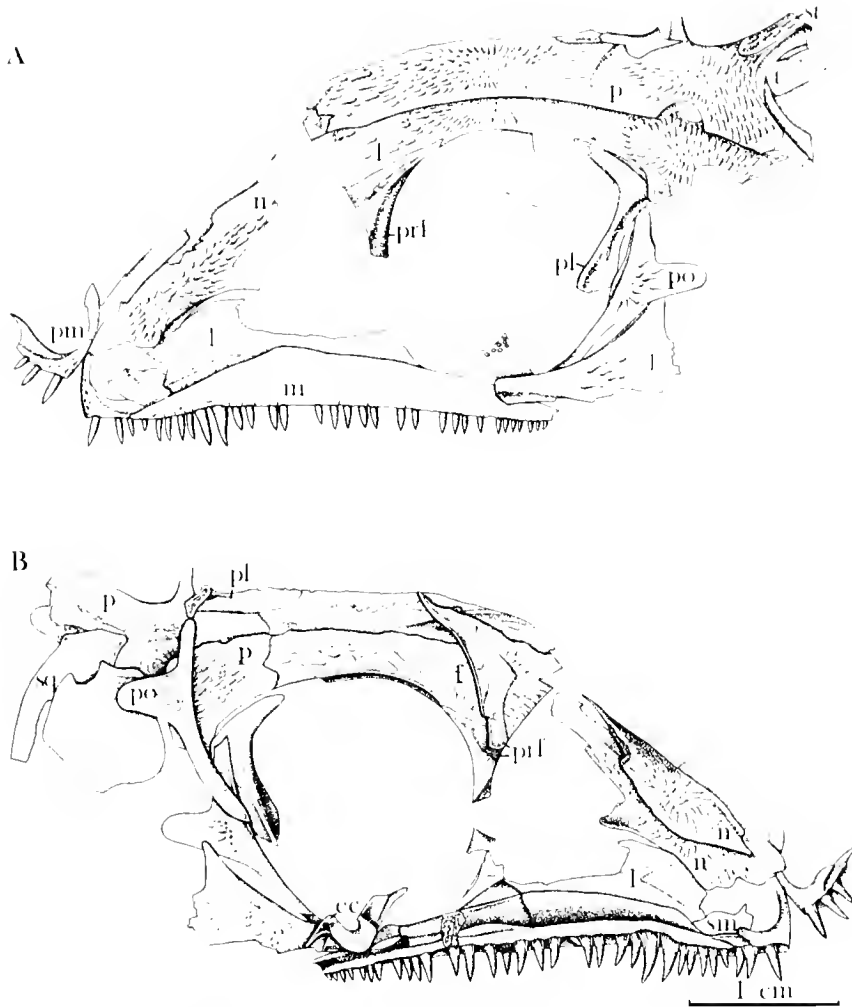
Fig. 8.—*Petrolacosaurus kansensis* Lane. Mature skull, KUVP 9952. The external (A) and internal (B) surfaces of the skull table and left cheek are shown, but the preserved part of the right cheek is exposed only in lateral view. See Fig. 2 for key to abbreviations.

(Fig. 12 and 13) is a large sheet of bone that extends from the naris to the orbit. From its broad contribution to the narial border, the laterally exposed surface of the lacrimal extends slightly upward, increasing its width posteriorly, and forming the anteroventral border of the orbit. Its suborbital ramus extends far posteriorly and makes contact with the anterior end of the jugal. The ventral border of the lacrimal is overlapped by the maxilla from the region of the canines to the posterior tip of the bone, as seen in the right side of the skull in KUVP 33607. Consequently, less than half of the height of the suborbital ramus is seen in lateral view.

The right lacrimal, in KUVP 33607, shows three foramina that open into the orbit. Two large lacrimal puncti are situated in a deep, conjunctival groove near the lateral border of the lacrimal. The groove is partially exposed in lateral view. A much smaller foramen is visible on the medial surface of the suborbital ramus that may have carried the anterior orbital artery, much as in the primi-
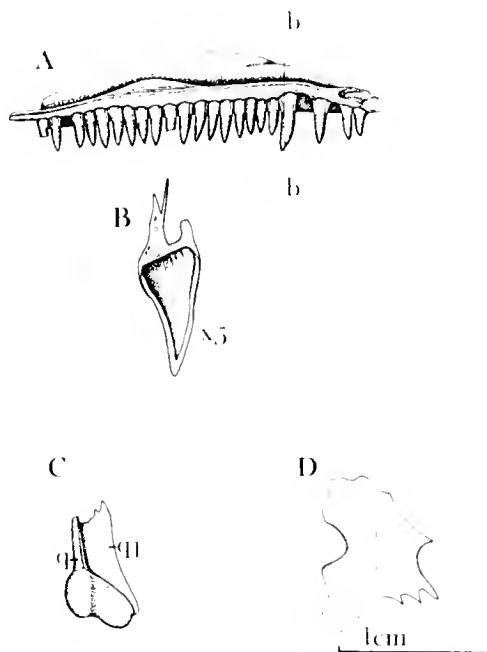
FIG. 9.—*Petrolacosaurus kansensis* Lane. (A) Isolated left maxilla, KUVP 33602, exposed in medial view, × 2. (B) Section through maxilla at b-b, × 5. (C) Left parietal from a poorly preserved skull, KUVP 9959a, exposed in ventral view, × 2. (D) Quadrate and quadratojugal from poorly preserved, immature skull, KUVP 33603, exposed in partial ventral view, × 2. See Fig. 2 for key to abbreviations.

tive captorhinid *Eocaptorhinus laticeps* (Heaton, 1979). The lacrimal canal is completely enclosed within the lacrimal bone.

The orbital margin of the lacrimal is strongly buttressed. At the level of the anterior border of the orbit, the lacrimal reaches the alveolar shelf of the maxilla and reinforces the maxillary process where it is sutured with the palatine. This is best seen in Fig. 8, where the suborbital ramus of the right lacrimal is exposed in medial view.

Nasals.—The nasals, exposed both ventrally and dorsally in KUVP 9952 and 33607, are paired bones lying along either side of the midline of the skull, between the premaxillae and the frontals; they form part of the skull roof in the antorbital area. The pair are sutured to each other along most of their length. Each nasal has a posterior process that is well preserved in KUVP 9959b, which diverges from the midline and covers part of the frontals dorsally. Anteriorly, the bone curves strongly down to receive the dorsal

process of the premaxilla. The remaining part of the anterior border is free and forms the dorsal border of the external naris. Laterally, the nasal is sutured to the lacrimal and the prefrontal. The lacrimal fits over a depression on the nasal, seen in KUVP 9952 (Fig. 8), whereas the prefrontal is attached to the ventral surface of the nasal.

The nasal is transversely convex (in cross-section) in the region where it is attached to the lacrimal, forming a dome over the nasal capsule. On the ventral surface, a prominent ridge runs anterolaterally from the posterior border.

Prefrontal.—The prefrontal, seen in lateral view in KUVP 9952 and 33607 and in dorsal view in KUVP 33606, is a triangular bone with an anterior plate that forms a wedge between the nasal and the lacrimal, and a thickened posterior ridge that forms the anterodorsal border of the orbit.

The anterior plate is a thin dorsoventrally convex sheet of bone, partially overlapped by

FIG. 10.—*Petrolacosaurus kansensis* Lane. Skull and lower jaws of young adult, KUVP 33608, × 2. The slightly disarticulated palate and braincase are exposed in dorsal view by loss of skull table. Part of the cheeks and the left parietal are exposed in internal view. See Fig. 2 for key to abbreviations.

the lacrimal and nasal. A heavily sculptured ridge that runs from the anterior plate to the orbital margin separates the lateral and dorsal aspects of the skull in the antorbital region. A heavy posterior thickening of the prefrontal forms the anterodorsal angle of the orbit.

The thickened dorsal orbital rim portion of the prefrontal extends far posteriorly and is sutured medially to the frontal in a well developed tongue and groove joint. The dorsal orbital margin is rugose and probably served as an attachment for part of the orbital fascia.

The prefrontal extends medially along its anterior orbital rim portion to form the vertical edge to which the orbitonasal membrane

was probably attached. A well developed ventral process of the prefrontal orbital ridge is strongly sutured to the medial surface of the thickened orbital rim portion of the lacrimal. The prefrontal is heavily sculptured near the orbital rim.

Frontal.—The frontals are the third in the series of paired bones lying along the midline of the skull. Each is a long prominent bone that lies on the dorsal surface of the skull. In KUVP 33606 (Fig. 11) the two frontals are joined to each other along most of their length in a slightly wavy tongue and groove suture. Each is bounded anteriorly by the nasal and laterally by the prefrontal and postfrontal. Between the latter two elements the
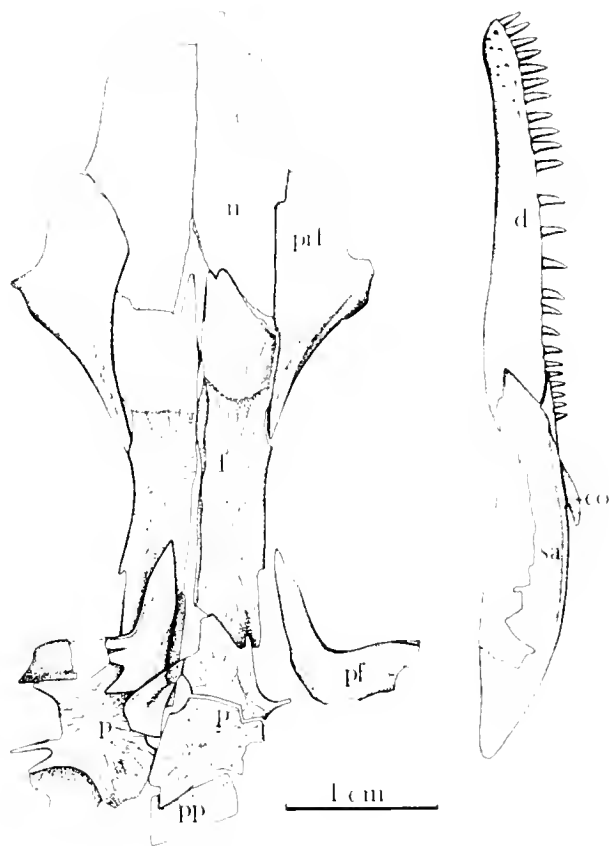
Fig. 11.—*Petrolacosaurus kansensis* Lane. Mature skull and left lower jaw, KUVP 33606, × 2. Part of the dermal skull roof is exposed in dorsal view, in almost perfect association; partial left lower jaw is seen in lateral view. See Fig. 2 for key to abbreviations.

frontal forms the orbital margin, and is slightly rugose to provide better attachment for the orbital fascia. Posteriorly, the frontal interdigitates with the anterior margin of the parietal. The frontal forms a wedge, posterolaterally, which partially separates the postfrontal and parietal. The suture between the postfrontal and the frontal is also of the tongue and groove type, similar to the suture between the prefrontal and frontal. In lateral view, the frontal is convex in outline, following the curve of the dorsal margin of the orbit. In cross-section, the frontal is slightly convex over the orbit. As seen in KUVP 9952 (Fig. 8b), the frontal has a strongly developed ridge on its ventral surface that runs the length of the bone, roughly parallel to the midline. It is to this ridge that both the pre-

frontal and the postfrontal are attached in order to brace the anterodorsal and posterodorsal corners of the orbit. This ridge is most pronounced over the orbit.

Parietal.—The parietal in *Petrolacosaurus* is readily distinguishable from that of captorhinomorphs and pelycosaurs because it forms part of the border of a well developed superior temporal fenestra. It resembles the parietal of other "eosuchians" and of araeoscelids. The description given here is based on well preserved parietals in KUVP 9951, 9952, 9959a, 33606, and 33607, and on isolated single elements in KUVP 9950, 33603, and 33604. Along the anterior part of its lateral border the parietal forms an "L" shaped suture with the postfrontal and a well developed lateral process that joins the postorbital and

forms the anterodorsal rim of the upper temporal fenestra. The central portion of the lateral border of the parietal is deeply concave and forms the dorsal rim of the superior temporal fenestra. The remaining portion of the lateral border is formed by a narrow wing that is directed posterolaterally and gently ventrally beneath the supratemporal to reach the squamosal. This wing is deeply excavated on the dorsal surface in order to receive the elongate supratemporal.

The posterior margin of each parietal is deeply embayed between the posterolateral wing and the midline. At the midline the two parietals form a posteriorly directed nuchal crest. At the occipital border the parietal appears to have a narrow sheet of bone that extends ventrally onto the occipital surface to support the postparietals and tabulars (Fig. 8a). The nearly straight interparietal suture is interrupted by the large, round pineal foramen.

The parietal is gently convex anteroposteriorly; the downward slope is evident in lateral view (Fig. 2).

In one specimen KUVP 9959a (Fig. 9c), a parietal, badly worn at the edges, has been preserved in ventral view. It reveals a slight longitudinal crest about halfway from the midline to the upper temporal fenestra. This crest presumably marked the position of the cartilaginous taenia marginalis of the chondrocranium and the point of attachment of the supraoccipital. Lateral to this crest the ventral surface of the parietal has a gently convex ridge that follows the medial margin of the upper temporal fenestra and extends onto the posterolateral wing of the bone. From this ridge to the temporal opening the parietal becomes progressively thinner.

Postparietal.—The postparietal, preserved only in KUVP 33606 (Fig. 11), is completely restricted to the occipital surface. It is only slightly visible in dorsal view. The element retains its primitive reptilian relationships—a paired bone in contact with the parietal, tabular, and supraoccipital.

Supratemporal.—A right supratemporal is only partially preserved in KUVP 9952 (Fig. 8). Its configuration can, however, be established on the basis of the deep, narrow groove on the posterolateral process of the parietal and on the posterodorsal aspect of the squamosal, in which this element lay. As in all captorhinomorphs were this element is preserved, the supratemporal in *Petrolacosaurus* is a long, narrow, slightly curved bone that lies on a process separating the superior temporal fenestra from the occipital surface of the skull. Posteriorly, it is anchored by a depressed facet on the posterodorsal corner of the squamosal. This indicates that the supratemporal probably serves to strengthen the parietal-squamosal contact, bracing the posterodorsal corner of the skull roof against the pull of adductor muscles.

Tabular.—The tabulars, as seen in KUVP 9952, are relatively small, elongate bones, completely restricted to the occipital surface. This element, although much reduced, retains its primitive relationships through contacts with the postparietal, parietal, supratemporal, and probably with the supraoccipital and squamosal. As reconstructed, the tabular forms a small part of the border of the posttemporal fenestra.

Postfrontal.—The postfrontal, seen in external and internal views in KUVP 9952 and 33607, is a relatively large, "L"-shaped bone that forms the posterodorsal margin of the orbit and has a long ramus lateroventrally beneath the postorbital. The postfrontal, as reconstructed, is a sharply convex bone, with most of the medial portion occupying a dorsal position while most of the lateral ramus extends down on the cheek. Its anterior apex fits into a small slot on the frontal. The medial border of the postfrontal extends far posteriorly, bound by the frontal and the parietal. The shape of the area of attachment of these two bones can be seen best in KUVP 33606 (Fig. 11). The angle between the medial and posterior edges of the postfrontal is close to 90 degrees. This corner of the bone is wedged deeply within the parietal, and the articulation is reinforced

FIG. 12.—*Petrolacosaurus kansensis* Lane. Mature skull and lower jaws with articulated cervical vertebrae, and an isolated right clethrum, KUVP 33607, × 2. The component skull elements are disarticulated, and compressed into a single plane. The right mandible and the vertebrae are exposed in lateral view. See Fig. 13 for opposite view of same specimen. See Fig. 2 for key to abbreviations.
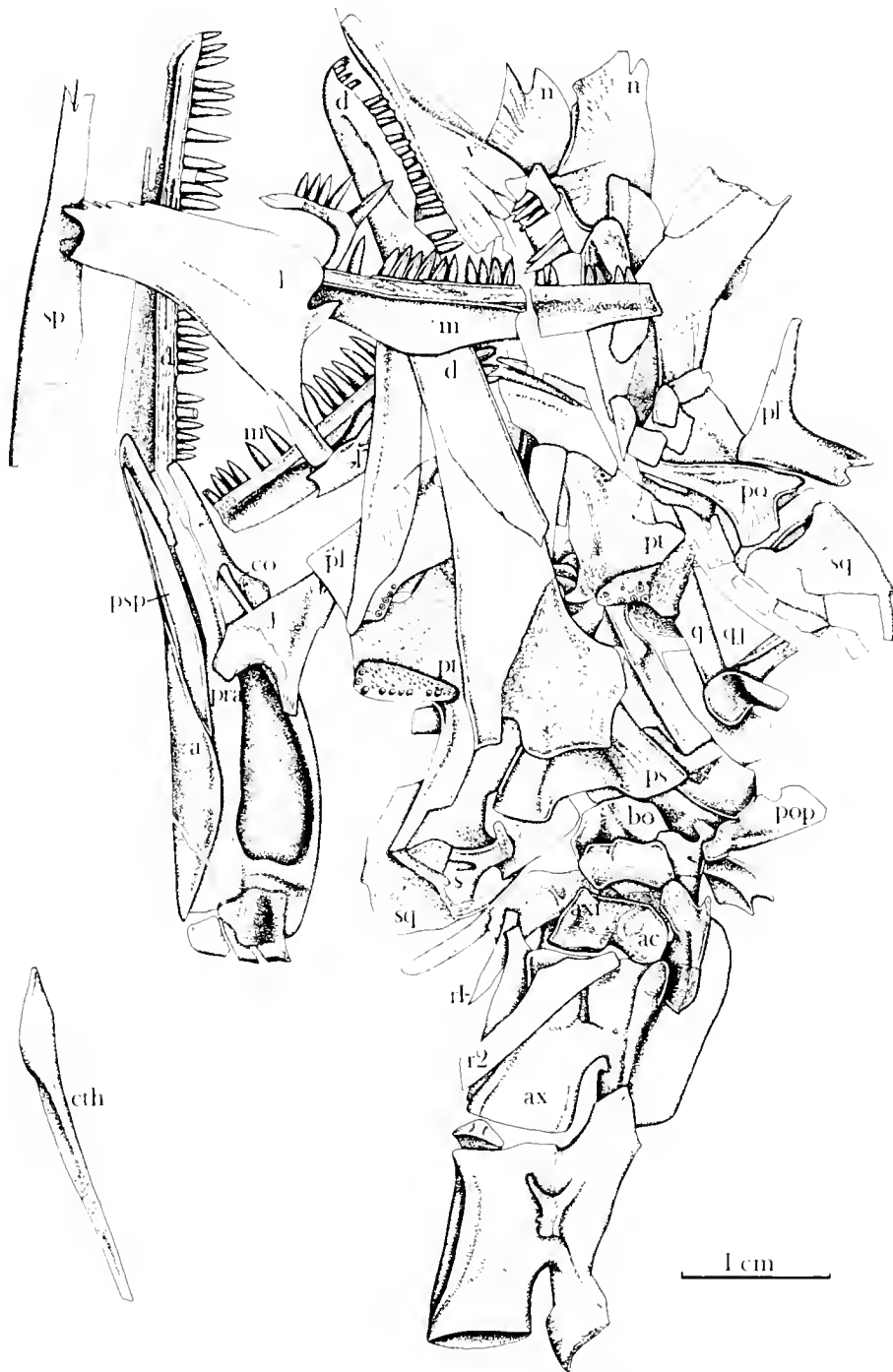
FIG. 13.—*Petrolacosaurus kansensis* Lane. Mature skull and lower jaws with articulated cervical vertebrae, and an isolated right cleithrum, KUVP 33607, × 2. The component skull elements are disarticulated, and compressed into a single plane. The left mandible lies over the palate. See Fig. 12 for opposite view of same specimen. See Fig. 2 for key to abbreviations.

by a facet in the parietal that supports the posterior edge of the postfrontal from underneath. The ventrolateral ramus of the postfrontal fits under and follows the curve of the upper half of the postorbital.

The ventrolateral process of the postfrontal appears to be massive and triangular in cross-section. The postfrontal in KUVP 9952 (Fig. 8) has a well exposed ventrolateral ramus. In lateral view, a slight ridge is present close to the orbital margin. The medially inflected anterior margin of the postorbital fits over this ridge and covers the ramus of the postfrontal. In medial view, the postfrontal shows a well developed ridge that extends to the ventral tip of the bone. This ridge on the postfrontal is equivalent to the medially extending plate of bone seen on the prefrontal. Both ridges reinforce the orbital margin.

Postorbital.—The postorbital, exposed in lateral view in KUVP 33607 and in both lateral and medial views in KUVP 9952, has the triradiate configuration typical of diapsid reptiles. Although slightly disarticulated from the rest of the skull elements, its relationship to the surrounding bones can be established with confidence. The ventral process of the postorbital extends around the postfrontal covering much of its surface and entering the posterior orbital border. This process reaches far ventrally to attach to the anterodorsal facet of the jugal. The length and surface detail of the ventral process of the right postorbital in KUVP 9952 indicates that almost one-half of this process was applied to the inside surface of the jugal, and must have extended near to the jugal-ectopterygoid suture. The concave anterior rim of the postorbital is thicker than the rest of the bone and is medially inflected. The posterior margin of the ventral process of the postorbital forms part of the anterior border of the lower temporal fenestra. The dorsal process forms the anterior border of the upper temporal fenestra and extends as a narrow slip of bone between the postfrontal and parietal. This dorsal process was flattened in both the right

and left postorbitals of KUVP 9952. In KUVP 33607 the right postorbital was also flattened, but the left retains much of its original shape (Fig. 13). The posterior process of the postorbital is sutured to the squamosal and forms the anterior half of the intertemporal bar.

Jugal.—The jugal, exposed in lateral and medial views in KUVP 9951 (Fig. 6), 9952 (Fig. 8), 33608 (Fig. 10), and in KUVP 33607 (Figs. 12 and 13), forms part of the cheek region below and behind the orbit. Its triradiate configuration can be seen clearly in all specimens and is typical of forms with lower temporal fenestrae. The two ventral rami form not only the lower margins of the orbit and the lower temporal fenestra, but also the ventral border of the skull behind the maxilla. The suborbital ramus extends far forward to reach the posterior projection of the lacrimal. In both KUVP 9952 (Fig. 8) and KUVP 33607 (Fig. 12) the lateral surface of the suborbital ramus is deeply recessed close to the anteroventral border, indicating that in this region the jugal was partially covered laterally by the maxilla. The lower temporal ramus of the jugal, completely preserved only in KUVP 9951 (Fig. 6), is much wider than the other rami. It extends below the lower temporal fenestra, and probably attaches to the quadrato-jugal. The dorsal ramus of the jugal forms the lower part of the postorbital bar. The anterior border of this ramus bears a long groove that slants diagonally upward and backward. This groove receives the ventral process of the postorbital.

The orbital margin of the jugal is thickened on the medial surface. Immediately above the posterior end of the maxilla, this thickened region of the jugal has a well developed medially projecting tubercle that is sutured to a stout lateral process on the ectopterygoid. This tubercle, partially exposed in KUVP 33607, but also seen in KUVP 9951 and 9959a, provides the only contact between the palate and the jugal. The posterior ramus of the jugal is smooth and very thin.

Quadratojugal.—The quadratojugal, which is only partially preserved in KUVP 33603,

33607, and 33608 is a thin, elongate sheet of bone that forms the ventral border of the skull behind the jugal, and meets the squamosal behind the lower temporal fenestra. Although this bone is poorly preserved in all the above specimens, there is evidence to indicate that the jugal and quadratojugal attach to one another below the temporal fenestra. In KUVP 33608 (Fig. 10), the badly preserved jugal and quadratojugal appear to be in contact. In addition, the height and length of the quadratojugal, relative to the quadrate in the immature specimen KUVP 33603 (Fig. 9c), indicates that the quadratojugal extended far anteriorly below the lower temporal opening as a tall, thin sheet. The jugal also extends posteriorly as a relatively tall, thin sheet; its posterior outline is indicative of an overlapping suture with the quadratojugal. The quadratojugal, therefore, not only forms the ventral edge of the lower temporal fenestra, but also contacts the jugal. The quadratojugal wraps posteriorly around the dorsal process of the quadrate as indicated in KUVP 33603.

Squamosal.—Although seen in many specimens, the squamosal is incompletely preserved in all, and is therefore, difficult to interpret. The size and shape of the squamosals in KUVP 33607 and 33608 indicate that most of the cheek region behind the temporal fenestrae is covered by this large plate-like bone. The anterior portion of the right squamosal in KUVP 33607 (Fig. 12) shows very clearly that, as in all primitive diapsids, this bone forms the rounded posterior borders of the upper and lower temporal fenestrae and extends an anterior projection between the fenestrae to form the posterior portion of the intertemporal bar. Although incomplete, the posterior border of the squamosals in KUVP 9952 (Fig. 8b), 9959a and 33607 (Figs. 12 and 13) is sufficiently preserved to indicate that this element forms the rounded posterior border of the cheek region, as in primitive captorhinomorphs. In KUVP 33607 the long posterior strip of the right squamosal which is partly separated from the rest of the

bone, probably wrapped around the dorsal process of the quadrate to present in occipital view a narrow strip that forms the lateral border of the posterior temporal fenestra and may have also provided support for the tabulars. The posterior region of the squamosal is, therefore, similar in *Petrolacosaurus* and captorhinomorphs and more primitive than in all other diapsid reptiles, where the squamosal does not cover the dorsal process of the quadrate completely. In all known Permian and Triassic "eosuchians" it is the quadrate that forms the concave posterior margin of the skull and eventually the otic notch. There is no otic notch in *Petrolacosaurus, Araeoscelis* or primitive captorhinomorphs.

The shape and configuration of the preserved squamosals also indicates that, dorsally, this bone enters the superior surface of the skull, contributes to the medial edge of the upper temporal fenestra, supports the supratemporal, and comes in contact with the parietal. Ventrally the squamosal overlaps the quadratojugal.

The squamosal in KUVP 33607 is thickest at its center of ossification, which is located at the level of the intertemporal bar. From here the bone thins anteriorly and anteroventrally, but remains thick posteroventrally. The posterior border of the squamosal in KUVP 33604 and 33608 is also thick. At margins of the temporal fenestrae, the squamosal is very thin. The anteroventral corner of the squamosal is not preserved in any specimen.

DERMAL BONES OF THE PALATE

Vomer.—The vomers are best preserved in KUVP 33608 (Fig. 10) and KUVP 33607 (Figs. 12 and 13) where they appear as paired sheets of bone lying anteriorly along the midline of the palate. In ventral aspect the vomer is a long roughly triangular element, occupying 28 per cent of the total length of the skull. The entire lateral border of the vomer forms the medial rim of the internal naris. Anteriorly and posteriorly the vomer is sutured to the premaxilla and palatine, respectively. The two vomers are su-

tured to each other at the midline along two-thirds of their length. Posteromedially the vomers are separated along the midline by a narrow wedge-shaped anterior extension of the pterygoids.

Medially the vomer is strengthened by a longitudinal ridge on the dorsal and ventral surfaces (Fig. 10). The ventral ridge carries a row of large teeth that approaches but does not reach the premaxilla anteriorly. The posterior three-fourths of the ventral surface of the vomer is also covered by small denticles. The ventral surface is concave in cross-section. The lateral border of each vomer curves ventrally but is not ridged.

The dorsal surface of the vomer is more complex than the ventral, with a tall median ridge, a flat central surface and a longitudinal depression near the lateral rim (KUVP 33607, Fig. 13). The median ridge probably strengthened the contact between the vomers and supported the nasal septum. The flat dorsal surface of the vomer is narrow anteriorly but widens posteriorly, where it is partially covered by the large anterior process of the palatine. The longitudinal depression is a deeply concave surface, bound medially by a ridge that probably represents the medial boundary of the internal naris.

Palatine.—The palatine in KUVP 33608 (Fig. 10) and KUVP 33607 (Fig. 13) is a rectangular sheet of bone pressed against the lateral edge of the pterygoid. The shorter sides of the rectangle form the sutures with the vomer anteriorly and the ectopterygoid posteriorly. The long lateral side of the palatine extends in a wide process to the maxilla anteriorly as it does in *Youngina* and other diapsids. This massive process occupies one-third of the total length of the bone, its sutural surface is concave and scarred thus indicating that the palatomaxillary suture was heavily stressed. Between the maxillary process and the anterior suture with the vomer, the palatine forms the posterior margin of the internal naris.

Behind the maxillary process, the lateral edge of the palatine is free as in all diapsid reptiles, forming the anteromedial border of the suborbital fenestra. The palatine is not ridged along the rim of the fenestra. Small denticles, similar to those seen on the vomer, cover the surface of the palatine ventrally. In addition, a ridge with larger teeth runs diagonally across the palatine from its posteromedial corner toward the maxillary process.

In dorsal view, the palatine overlaps the lateral edge of the pterygoid and forms a stout process anteriorly over the dorsal surface of the vomer. The ectopterygoid apparently overlaps the posterior part of the dorsal surface of the palatine.

Ectopterygoid.—The left ectopterygoid is preserved in KUVP 9952 (Fig. 8). It is slightly out of position relative to the jugal and is seen in partial lateral view. A well developed process of the ectopterygoid projects laterally to articulate with a corresponding tubercle in the jugal, as it does in *Youngina* and other primitive diapsids. Anterior to this the lateral border of the ectopterygoid is free of sutural contact and forms the posteromedial and posterior boundary of the suborbital fenestra. Posteriorly, the ectopterygoid forms the anterior boundary of the subtemporal fossa; medially it is suturally attached to the pterygoid. Posteromedially this attachment is formed by a massive rounded abutting suture. Anteromedially, the ectopterygoid forms a small sheet of bone that extends onto the dorsal surface of the pterygoid. Anteriorly, the ectopterygoid overlaps the dorsal surface of the palatine.

Pterygoid.—The pterygoid, seen in both dorsal and ventral views in KUVP 8351, 33604, 33607 and 33608, is the longest bone of the skull, similar in most features to that in protorothyridids (Carroll and Baird, 1972). Although partially covered by other skull elements, its configuration and relationship to the surrounding bones can be established with confidence. The pterygoid has four processes common to all primitive reptiles: the palatal ramus, the transverse flange, the quadrate ramus, and the small process for the basipterygoid articulation.

The palatine ramus extends anteriorly from the region of the basipterygoid articulation to its acuminate termination between the vomers; it is widest where it articulates with the ectopterygoid. Along the posterior part of its medial edge the palatine ramus bounds the interpterygoid vacuity. A dorsally inflected ridge is present on the anterior one-third of the rim of the interpyterygoid vacuity. This inflected ridge continues anteriorly and helps to form a greatly strengthened suture between the pterygoids along the midline. The palatine ramus carries two longitudinal ridges on the ventral surface. These bear irregularly arranged teeth, up to 0.5 mm in diameter and not more than 1.0 mm in height. The medial ridge runs to the anterior tip of the pterygoid and is continuous with the tooth bearing ridge on the vomer. The shorter lateral ridge is continuous with a similar ridge on the palate. The rest of the palatal ramus of the pterygoid is covered with numerous small denticles, about 0.1 mm in diameter.

The transverse flange of the pterygoid extends anterolaterally at about 60 degrees to the sagittal plane. The flange slants ventrolaterally and extends below the lower margin of the cheek. The ventral surface of the flange is covered with a large number of irregularly arranged teeth of varying sizes. The largest teeth, located on the posterior rim of the flange, are up to 0.8 mm in diameter and 1.2 mm in height. The anterior portion of the flange is covered by smaller teeth.

The quadrate ramus, as seem in KUVP 8351 (Fig. 5a and b) is essentially a large vertical plate running posterolaterally from the basipterygoid region to the quadrate. The ventral edge of the quadrate ramus is thickened to form a ridge, above which the inner side is slightly concave. Posteriorly, the ramus is attached to the inner surface of the dorsal process of the quadrate. The contact between the two bones is extensive both anteroposteriorly and dorsoventrally. The laterodorsal surface of the quadrate ramus in

Fig. 5a shows an extensive area of attachment to the epipterygoid.

The basicranial process of the pterygoid is not well preserved in most specimens. In KUVP 33604 this process is exposed in dorsal view. It shows that the anteromedial part of the process has a small dorsally oriented articulating surface for the attachment to the basisphenoid. Most of the articulation, however, must have been provided by the epipterygoid.

OSSIFICATIONS OF THE PALATOQUADRATE CARTILAGE

Epipterygoid.—A small triangular piece of bone lying on the crumpled left quadrate ramus of the pterygoid in KUVP 8351 has been identified by Peabody (1952), with some misgivings, as the epipterygoid. This identification is of doubtful validity, however, and the element is not included in the reconstruction. In the same specimen, the dorsal expanse of the quadrate ramus of the right pterygoid is well preserved. Dorsomedially, the quadrate ramus of the pterygoid is strongly grooved at the level where the epipterygoid should be located. This attachment area is extensive, running posteriorly from the region of the basipterygoid process to the dorsal process of the quadrate. The conclusion that the epipterygoid extended so far anteriorly is supported by the fact that the articulating surface of the basiphenoidal process faces dorsolaterally and that the engaging process on the pterygoid is too thin in all the specimens, where this region is preserved, to provide support on its own. In addition, the epipterygoid in pelycosaurs and captorhinomorphs formed partly, or wholly, the articulation with the basisphenoid (Heaton, 1979).

The groove on the pterygoid for the base of the epipterygoid is not excessively long in *Petrolacosaurus* when comparison is made with other primitive reptiles. In *Dimetrodon* (Romer and Price, 1940, Pl. 7), for example, the base of the epipterygoid extends from above the dorsal process of the quadrate to

the interpterygoid vacuities, well past the level of the basicranial articulation.

Quadrate.—In *Petrolacosaurus*, the quadrate is a tall, well developed element, similar in configuration to that in captorhinomorphs and pelycosaurs. It is composed of a relatively flat sheet of bone that extends dorsally and anteriorly from the articular condyle. The articular area of the quadrate seen in ventral view in KUVP 33603, 33607 and 33608, consists of two subhemispherical surfaces, a lateral and a medial, separated by a groove. The lateral surface faces ventrally. The medial surface, on the other hand, faces ventrolaterally and is located farther anteriorly and ventrally than the lateral surface. The tall dorsal process of the quadrate preserved only in KUVP 33608, joins the quadrate process of the pterygoid anteriorly. The posterior margin of the dorsal process of the quadrate is covered by the squamosal and quadratojugal except in the region where the palatoquadrate foramen emerges, precluding the possibility of forming the margin of a squamate type of otic notch. The lateral surface of the quadrate forms part of the posteromedial wall of the adductor chamber.

OSSIFICATIONS OF THE BRAINCASE

Parasphenoid.—The parasphenoid is a median dermal element that provides a ventral cover for the braincase. In ventral view, the region of the parasphenoid ventral to the basisphenoid has the general outline of an isosceles triangle, typical of all primitive captorhinomorphs and early "eosuchians." The cultriform process, seen in both dorsal and ventral views in KUVP 9951 (Fig. 7) extends forward between the interpterygoid vacuities. It is "V"-shaped in section and bears a row of tiny denticles on its posteroventral aspect, as in primitive captorhinomorphs. The cultriform process probably supported the sphenethmoid.

The triangular portion of the parasphenoid hides most of the basisphenoid from ventral view. The ventral surface of the parasphe-

noid is covered with denticles at the level of the basisphenoidal tubera. The flanks of this rostrum are not well preserved. The location of the anterior internal carotid foramina cannot be established. The sides of the parasphenoid are formed by two rounded crests (Figs. 5b, 7a, and 13) that converge anteriorly and widen posteriorly. These crests, the cristae ventrolaterales, leave a wide depression on the ventral surface between them. The posterior end of these crests extend laterally beyond the basioccipital. The ventral surface of the parasphenoid between the two lateral ridges is formed by a thin sheet of bone underlying the anterior end of the basioccipital.

Exposed in dorsal view, the parasphenoid in KUVP 33608 has a thin sheet of bone on each side that probably extended dorsally (Fig. 10b) to attach to the prootic, contributing to the lateral wall of the braincase.

Basisphenoid.—In ventral view the basisphenoidal tubera project anterolaterally beyond the dermal parasphenoid. Each process has a slightly constricted waist and ends in a gently convex articular head. The articular area faces mainly anterodorsally and is little exposed in ventral view. Preservation of all the known basisphenoid-parasphenoid complexes either in dorsal or ventral views, makes identification of the suture between these elements impossible.

The basisphenoid in *Petrolacosaurus* can be seen best in dorsal view (Figs. 5a, 7b, and 10). The anterior portion of the basisphenoid forms a short rostral process. Its anterior termination is deeply incised between the cristae trabeculares to carry a small branch of the anterior internal carotid artery. The cristae trabeculares form the point of attachment of the trabecula communis to the basisphenoid.

Along the midline, just above the basisphenoidal tubera, a small pit in KUVP 9951 and 33608 (Figs. 7b and 10) probably marks the exits of the anterior internal carotid arteries, and their subdivisions, the pituitary arteries. A small transverse ridge separates this

region from the more posteriorly located sella turcica.

The basisphenoid supports a well developed dorsum sella, comparable in height to that in modern iguanid lizards and nearly as tall as in *Captorhinus*. The dorsum sella in *Petrolacosaurus*, exposed in KUVP 8351 and 33608 (Figs. 5a and 10) is a thin transverse sheet of bone strengthened laterally by the sellar processes. In both specimens the dorsum sella and the sellar processes have been crushed postmortally down onto the dorsal surface of the parasphenoid obscuring the cavum cranii, the largest concavity of the basisphenoid, where the anterior body of the medulla rested.

Basioccipital.—The short, stout basioccipital forms the ventral surface in the posterior portion of the braincase and the major portion of the occipital condyle. The ventral surface of the basioccipital is fully exposed posteriorly; its anterior portion, however, is covered by the posterior end of the basal plate of the parasphenoid. The well developed basioccipital tubercle, which forms most of the exposed ventral surface of the basioccipital, has a transverse ridge anteriorly between the cristae ventrolaterales of the parasphenoid, and a longitudinal ridge that extends along the midline to the occipital condyle. The margins of this tubercle probably formed the anterior and medial limits of the M. rectus anterior insertion.

Unlike those of pelycosaurs and captorhinomorphs, the basioccipital in *Petrolacosaurus* is not completely covered dorsally by the exoccipitals. The latter do not join at the midline to exclude the basioccipital from the floor of the foramen magnum.

Exoccipital.—In posterior view the exoccipital has a wide base that forms the dorsolateral part of the condyle. Above the condyle, an ascending process runs up along the side of the foramen magnum and is applied dorsally to the ventral edge of the supraoccipital. The posterior surface of the ascending ramus bears a facet for the proatlas. Between this and the main body, the

exoccipital forms the medial border of the vagus foramen. Below this foramen, and slightly medially, are two small hypoglossal foramina. At the base, the pair of exoccipitals approach each other but do not join at the midline (KUVP 33608, Fig. 10).

Prootic.—The prootic is the least well known element of the braincase in *Petrolacosaurus*. This element, preserved only in KUVP 9951, is similar in outline to that of *Captorhinus* (Price, 1935).

Supraoccipital.—The supraoccipital, also exposed in KUVP 9951 and 33607, forms the broad occipital plate. It not only forms the arched roof of the foramen magnum but also extends down on both sides to the exoccipitals.

Dorsomedially, the postparietals overlie the process of the supraoccipital that extends to the parietals. Dorsolaterally, the tabular covers the slightly ridged process of the supraoccipital that extends to the squamosal-parietal suture.

Posteriorly, the supraoccipital bears a pronounced median ridge separating the probable insertions of the M. recti capiti posterior. This ridge runs from the postparietals to the foramen magnum, where it fans out laterally. In KUVP 9951, the supraoccipital has been crushed flat, exaggerating the lateral extent of this bone. Normally the two dorsolateral "wings" of the supraoccipital, exposed in Fig. 7, face mostly laterally and only slightly posteriorly; they formed the lateral wall of the braincase behind the prootic.

Opisthotic.—The opisthotic, also found only in KUVP 9951 and 33607, is partially preserved. The available material indicates that, as in pelycosaurs, *Araeoscelis* and *Youngina*, the opisthotic in *Petrolacosaurus* forms an ossified paroccipital process. Unlike *Araeoscelis*, however, this process did not quite reach the quadrate. In addition, a ventral process of the opisthotic extended down along the lateral margin of the exoccipital-basioccipital complex. The level of its ventral termination is, however, indeterminate.

Stapes.—The stapes preserved in KUVP

8351 and 33607 retain the pattern found in all primitive Paleozoic reptiles. It is a relatively massive bone consisting of a large proximal head and a gently tapering columellar process pierced by the stapedial foramen. The proximal head is poorly preserved, but it probably consisted of a footplate and a dorsal process. The distal tip of the columella in KUVP 33607 is slightly expanded and its surface is unfinished.

MANDIBLE

Dentary.—This long, unusually slender element, best preserved in KUVP 33606 and 33607, carries the mandibular tooth row and occupies a considerable area of the outer surface of the mandible. Anteriorly, it excludes the splenial from the lateral surface. It is bounded posteroventrally by a narrow slip of the splenial. Posteriorly, the dentary covers the angular and surangular and narrows dorsally. Its posterior tip lies near the dorsal margin of the mandible, covering most, but not all, of the coronoid. The single lateral tooth row is supported by a medially directed shelf on the internal surface of the dentary, close to the dorsal edge of the bone. The lateral margin of this shelf is, as in the case of the maxilla, much higher than the medial one. Anteriorly, the shelf forms most of the symphysial surface. This area is exposed only in KUVP 33607; it is quite small and bears no marked ridges. Behind the symphysial area, the dentary is completely exposed medially to the level of the eighth tooth. Further posteriorly, the medially directed shelf is strongly ridged, indicating the area of attachment of the splenial and coronoid. Below the shelf, the dentary is strongly excavated for the channel of the Meckelian canal; the dentary forms the roof and lateral wall of the canal in its anterior portion. In KUVP 33607 there are 28 teeth attached to the dentary with shallow alveoli for five more.

Angular.—The angular, also preserved in KUVP 33607, is a large "V"-shaped element, occupying part of the medial and lateral surfaces of the mandible. It forms the ventral portion of the mandible posterior to the dentary and splenial, and continues back to the end of the jaw as a deep keel below the surangular and prearticular. This bone is overlapped anterodorsally by the dentary, but it overlaps the surangular and articular on the lateral surface and the prearticular on the internal surface of the mandible. Below the prearticular fossa the angular forms the floor of the Meckelian canal and part of the lateral wall.

Surangular.—The surangular, also exposed in KUVP 33607, is a simple sheet of bone that occupies the posterior portion of the mandible. Its lateral exposure is relatively small; it is overlapped by both the dentary and the angular. Internally, it is overlapped by the posterodorsal process of the coronoid. Posteriorly, the surangular has a large exposure along the lateral wall of the adductor fossa. The upper edge of the bone is somewhat thickened; posteriorly, it swings inward to attach to the articular and form the posterior wall of the fossa.

Splenial.—The splenial, as seen in KUVP 33607 and 33608, forms most of the anterior portion of the medial mandibular surface. The lateral exposure of this bone is limited to a narrow strip below the posterior part of the dentary. Anteriorly, the splenial is in contact with the dentary above and below the anterior opening of the Meckelian canal. This contact is maintained for some distance posteriorly with the splenial forming the medial wall and floor of the canal. Posterodorsally, the splenial covers the anterior projection of the coronoid. A posteriorly directed thin sheet of the splenial covers part of the prearticular and posterior splenial and comes in contact with the angular.

Posterior splenial.—A small elongate sheet of bone, that tapers to a point both anteriorly and posteriorly, lies on the medial surface of the mandible in KUVP 33607. Anteriorly, a large portion of this bone was probably covered by the splenial. It is sutured to the prearticular dorsally and the angular ventrally. This bone may be comparable to the posterior

splenial seen in some amphibians; it presumably formed part of the medial wall of the Meckelian canal. A posterior splenial has not been reported in other Paleozoic reptiles.

Prearticular.—The prearticular, a major element on the inner surface of the mandible, is well preserved only in KUVP 33607. Posteriorly it is applied to the inner surface of the articular. The suture between these two bones is not visible. The conjoined edges of the prearticular and articular are drawn out medially to form a small shelf at the posteroventral corner of the adductor fossa. From this area, the prearticular extends anteriorly as a sheet of bone along the inner surface of the mandible, forming the medial margin of the adductor fossa and most of its medial wall. The prearticular is overlapped below by the angular and the postsplenial. Anteriorly, the prearticular is covered by the posterior end of the splenial. Anterior to the adductor fossa, the prearticular is again drawn out medially to form a shelf ventral to the coronoid. In this region, the prearticular forms part of the medial wall of the Meckelian canal.

Coronoid.—Only a single edentulous coronoid is present in *Petrolacosaurus*. In KUVP 33607 the anterior half of this bone is a thin sheet, applied to the medial surface of the dentary below the marginal tooth row, and in contact with the splenial anteriorly and the prearticular ventrally. A thicker area forms the anterior margin of the adductor fossa and part of its dorsal rim. The posterodorsal end of the bone lies beneath the surangular, on the outer part of the mandible.

Articular.—The articular joins the lateral and medial walls of the adductor fossa and forms the articulating surface with the quadrate. This surface consists of two parallel, elongate concavities, the inner groove lying at a lower level than the other. Externally, the articular bone is almost completely covered by the surangular and angular, but forms the convex posterior end of the mandible. There is no distinct retroarticular process. What looks like a small retroarticular process in

KUVP 33607 is actually part of the rounded posterior end of the articular that was pushed posteriorly when the lower jaw was crushed. A short angular process extends medially and somewhat ventrally from the articular surface of the articular, probably for the insertion of the superficial pterygoideus musculature.

DENTITION

The teeth in *Petrolacosaurus* are simple conical structures. In both the upper and lower jaws there is a marginal series of subthecodont teeth. There are also many palatal teeth. The marginal teeth, arranged in a single row, are slightly compressed and sharply pointed. Towards the tips, the teeth bend slightly posteriorly and are marked by longitudinal grooves. This longitudinal grooving, or fluting, occurs only towards the tip and is often seen in well-preserved Paleozoic reptiles.

On the premaxilla, the anteromedial tooth is the largest. Posterolaterally, the premaxillary teeth show progressive diminution in size. The first three teeth tend to be inclined slightly anteroventrally. Two teeth in the anterior portion of the maxilla are larger than the others and hence may be designated as caniniform teeth. This is a primitive amniote condition that persists in many Permian reptiles. In *Petrolacosaurus*, the caniniform teeth are only slightly longer than the first premaxillary teeth. These relatively large teeth, the two to four smaller premaxillary teeth, and the four pre-caniniform teeth create a seemingly efficient food trap. The post-caniniform teeth, although definitely smaller than the caniniform teeth, remain quite large until well posteriorly in the series; only the final eight to ten teeth show successive diminution in size. The upper tooth row continues back to the posterior extremity of the maxilla.

The mandibular marginal dentition is basically homodont with reduction in tooth height only in the last five to seven teeth (KUVP 33606, Fig. 11). The lower tooth row does not seem to extend back to the extreme

end of the dentary. The teeth at the level of the maxillary caniniforms are slightly longer than the rest of the mandibular teeth. Although the anterior three teeth on the dentary point slightly anteriorly as on the premaxilla, they show slight progressive diminution forward.

In both the upper and lower jaws, the teeth sit on a medially directed shelf and are supported laterally by a thin sheet of bone. In medial view, the teeth show slight vertical ridging close to the base. Cross-sectional views of the maxillary teeth (Fig. 9b) show that they are essentially thin walled cones with an open base. Large pulp cavities extend close to the tip of the teeth. The teeth sit in shallow pits on the jaw. Implantation has been strengthened by a thin sheet of bone that extends from the circular margin of the pit onto the lateral surface of the tooth base and is solidly fused to it. This fusion gives the appearance of ridging both on the outside and the inside of the teeth close to the base.

Palatal teeth occur on the pterygoids, palatines, vomers and the parasphenoid. Relatively large teeth (up to 1.2 mm in length), irregularly distributed along ridges on the palate, extend in three directions from the basipterygoid area. A variable number of large teeth extend laterally onto the transverse flange of the pterygoid. Another group of slightly smaller teeth extend diagonally across the pterygoid and palatine. A third group extends anteriorly along the medial edge of the pterygoid and the vomer.

Numerous small teeth (about 0.3 mm in length) are rather evenly distributed over most of the palatal plate between the rows of larger teeth. The teeth on the parasphenoid are also quite small. A number of broken teeth indicate that both large and small palatal teeth have well developed pulp cavities. There are no teeth on the inner surface of the mandibles.

Sclerotic Plates

Series of thin translucent sclerotic plates lie in the orbit of the skulls in KUVP 9952

and 33606. The seven plates in the orbit of the skull in KUVP 33606 are only partially preserved, but they appear rectangular and do not overlap one another. After the better preserved plates in KUMNH 9952 (Fig. 8a) were covered with a resin imbedding compound, the outline of what appear to be five small, triangular plates were found wedged between five larger, nearly rectangular plates. In both specimens the sclerotic plates were flat, but this may be due to crushing.

Vertebrae

Notwithstanding certain specializations, the vertebral column of *Petrolacosaurus* retains most of the general characteristics seen in the captorhinomorphs. Each segment of the column includes a centrum, neural arch and intercentrum. Each centrum has the basic hourglass configuration, with expanded hollow ends facing adjacent centra and a narrow waist. A ventral longitudinal ridge extends between the anterior and posterior ends of the centrum to strengthen the hourglass structure. Anterodorsally, thickened areas serve as points of attachment for the neural arches. Thus, all the centra except the first are amphicoelous and all are notochordal. The notochordal canal is strongly constricted at the middle of each centrum. The neural arches are fused solidly to the centra and sutures have been obliterated. The articular areas of the zygapophyses are simple plane surfaces, somewhat tilted from the horizontal. The intercentra are well developed.

A presacral vertebral count of 26 is definitely established on the basis of several articulated specimens. There are six cervical vertebrae that form a distinct neck region. The calculated length of the cervical series in KUVP 9951 is about 72 mm; the calculated length of the dorsal series in the same individual is about 192 mm. There are two sacral vertebrae as is typical in most primitive reptiles. An approximate count of 60 to 65 for the number of caudal vertebrae is based on two partial specimens, KUVP 1427 and KUVP

1428 (Peabody, 1952, Figs. 2 and 4). The distal part of the tail is composed of at least twelve spool-shaped centra without neural arches. The ealeulated length of the eaudal region based on these two immature specimens is about 315 mm.

CERVICAL VERTEBRAE

Atlas-axis complex.—The proatlas (Fig. 14) is a relatively small but robust element. The two elements of the pair do not appear to be in eontaet. There is a rudimentary neural spine on eaeh element and a small posterior zygapophysis that articulates with the atlas.

The articulating surfaee of the posterior zygapophysis faces medially so as to be aligned almost with the saggital plane. An anterior zygapophysis is also present but faces forward to articulate with the corresponding facet on the exoccipital. The proatlas in *Petrolacosaurus* is similar in outline to the proatlas in the primitive captorhinomorphs *Hylonomus* and *Paleothyris*; it is much shorter than the same element in the pelycosaur *Ophiacodon*.

The atlas in *Petrolacosaurus* includes four elements: the intercentrum, two neural arches and the centrum. The intercentrum
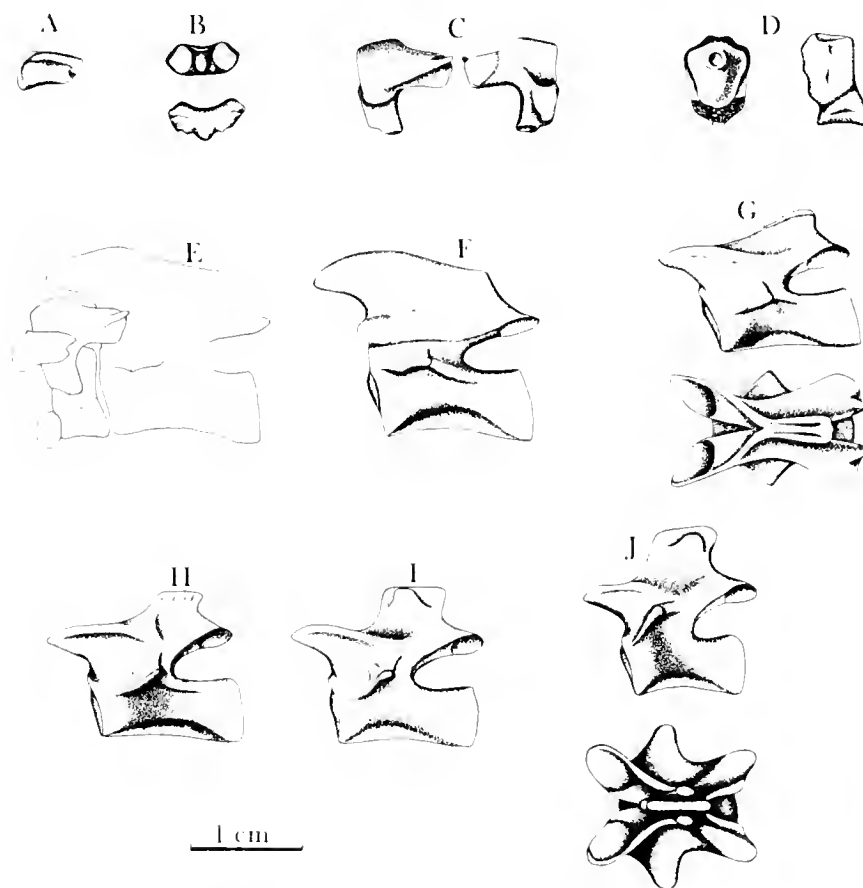
Fig. 14.—*Petrolacosaurus kansensis* Lane. Cervieal vertebrae, all × 1.5. (A) Lateral view of left proatlas, KUVP 33607. (B) Ventral and anterior views of atlantal intereentrum, KUVP 33604. (C) Lateral and medial views of left atlantal neural arch, KUVP 33604. (D) Anterior and lateral views of atlantal eentrum and fused axial intercentrum, KUVP 33604. (E) Outline of the atlas-axis eomplex, based on KUVP 33604 and 33607. (F) Lateral view of axis, KUVP 33604. (G) Lateral and dorsal view of third eervical vertebra, based on KUVP 9951 and 9956. (H-I) Lateral view of fourth and fifth eervieal vertebrae, KUVP 9951. (J) Lateral and dorsal views of the sixth cervieal vertebra, based on KUVP 9951 and 9956.

has the usual crescentic shape, but is slightly larger than its counterparts in the remainder of the column with the exception of the axial intercentrum. A strongly concave anterior surface receives the ventral portion of the condyle. The posterior surface, which is less deeply cupped, is apposed to the axial intercentrum. Laterally there is a small articular surface on each side for the capitulum of the first cervical rib. This is a rather primitive feature seen in captorhinomorphs and pelycosaurs. Ventrally the intercentrum has the longitudinal ridge seen in the other cervical intercentra.

The atlantal neural arch (Figs. 12, 13 and 14) is a paired structure. There is a thin shelf of bone above the neural canal, but the two sides apparently are not in contact. The postzygapophysis extends far posteriorly to articulate, by a medially directed face, with the prezygapophysis of the axis. A posteriorly directed spine, external to this facet, extends for a short distance beyond the point of articulation with the axis. At the anterodorsal angle of the atlantal neural arch a roughly circular surface faces laterally and slightly dorsally to connect with the proatlas. Anteriorly, the neural arch articulates with the dorsolateral portion of the condyle. A wide ventral process descends over the lateral surface of the atlantal centrum and articulates with it via a medially directed pedicel. The base of the neural arch has a small ventrally directed process for articulation with the tuberculum of the atlantal rib.

The atlantal centrum is well developed although considerably smaller than other presacral centra. Dorsally, it is gently grooved to form the floor of the neural canal. Anterodorsally, there is on both sides a well developed articulating surface for the pedicel of each neural arch. Behind this area the upper and lateral surfaces of the centrum are free. In immature specimens (Peabody, 1952, Fig. 3), the centrum has, in anterior view, the shape of an inverted "U" that sits loosely on the axial intercentrum. In more mature specimens (KUVP 33607, Fig. 12), however, the

notochordal canal is completely closed by a more fully ossified centrum. In these mature individuals the upper part of the anterior surface surrounds the relatively small notochordal pit and articulates with the central portion of the condyle. The posterior surface of the centrum articulates with the upper half of the axial centrum and is of normal construction.

Ventrally, the atlantal centrum sits on the axial intercentrum and does not reach the ventral surface of the column. Even in mature specimens, although the above two elements are fused, the areas of fusion are marked by a wide band of unfinished bone. A somewhat similar pattern is seen in *Heleosaurus* (Carroll, 1976).

The axial intercentrum is relatively large, exceeding in length all the other intercentra. This intercentrum is more plate-like than crescentic and has the well developed longitudinal ridge seen in the atlantal intercentrum. In lateral view, it has the shape of a right angle triangle, the sides of the 90 degree angle facing posteriorly and ventrally. There are no obvious facets for rib articulation at the lateral margins of the element as seen on the atlantal intercentrum.

The axial centrum-neural arch complex, well preserved in KUVP 33607 and 9951, is a robustly built structure in *Petrolacosaurus*, lying at the functional end of the vertebral column and linking it to the skull. Its dual function is clearly indicated by the form of the axial neural arch (KUVP 33607 and 9951), which posteriorly is not greatly different from that of the succeeding cervical vertebrae. Anteriorly, it is highly modified to provide origins for muscles inserting on the occipital region of the skull and to support the skull through the remainder of the atlas-axis complex. The neural spine is strongly built, unusually thickened and elongated anteroposteriorly to a length about equal to that of the centrum below. The posterior border is heavy, and in one specimen small processes near the top project posteriorly, possibly marking the origin of the M. spinalis capitis.

The massiveness and the anteroposterior elongation of the spine unquestionably provides added support to such muscles as the M. rectus capitis and the M. obliquus capitis. The anterior portion of the neural spine projects anteriorly dorsal to the posterior part of the atlantal centrum and neural arches, as in *Araeoscelis*, and other primitive reptiles.

The postzygapophyses of the axial neural arch are normally developed; the prezygapophyses are weak, project little from the surface of the arch, and face laterally as well as slightly upward. A ridge runs posteriorly from the prezygapophyses. The transverse process or diapophysis is stoutly built, although not greatly elongated, and originates far ventrally on the neural arch. It projects ventrolaterally at about 45 degrees to the sagittal plane. The diapophysis is buttressed by converging ridges from the neural arch and centrum. The articular surface is small, however, and keyhole-shaped.

The neural arch contributes significantly to the anterior centrosphene, which has a much greater vertical extent than the posterior articulation. This greater anterior articulating surface provides sufficient contact for the combined height of the atlantal centrum and axial intercentrum. This basic pattern is seen in such diverse forms as *Ophiacodon*, *Heleosaurus*, *Araeoscelis*, *Paleothyris*, *Platecarpus*, and *Gavialis*. The construction of the atlas-axis complex indicates that movement of the head was concentrated at the articulation between the condyle and the atlantal elements. There appears to have been little movement between the atlantal centrum-axial intercentrum and the axial centrum.

The cervical vertebrae in *Petrolacosaurus* (KUVP 9951, 9956) are conspicuous in their degree of elongation. A number of later but still relatively primitive reptiles, such as *Araeoscelis*, *Prolacerta*, *Macrocnemus*, and *Tanystropheus* are also long-necked.

In the anterior part of the vertebral column, an abrupt elongation of centra starts with vertebra 7 and continues to the axis. The centrum in vertebra 7 is 1.25 times longer

than the average mid-dorsal centrum, and in vertebra 6, it is 1.35 times longer; the centra in vertebrae 2 to 5 are of equal length, being 1.55 longer than the average mid-dorsal centrum. All these elongate centra have a slightly smaller vertical diameter than the dorsal vertebrae. In all cervical vertebrae the anterior centrosphenes are inclined anteriorly. This inclination is most marked on the anterior cervical vertebrae, where the posterior centrosphenes are also tilted forward. This specialization in *Petrolacosaurus* would have permitted raising, and possibly maintaining, the head high above the ground.

There is no bevelling on the centra for accommodating the large intercentra; the latter were probably continued dorsally in cartilage. In all cervical vertebrae, the longitudinal ridge at the bottom of the centrum extends far ventrally, forming a strong keel, with its lateral surfaces concave in section. The keel of the anterior cervical vertebrae, forms a nearly straight line between the ends of the centrum, and is "V"-shaped in section. On the posterior cervical vertebrae this keel does not extend as far ventrally and tends towards a more rounded ventral margin.

The cervical neural arches are attached by a pair of pedicels to the anterior half of the centra. Anteriorly, the margin of the pedicels form the dorsal half of the centrosphene. Above the centrosphene, the anterior edge of the arch forms a slight notch before curving up and anteriorly beneath the prezygapophysis; this notch forms the posterior boundary of the intervertebral opening. The dorsal margin of the posterior end of the pedicel is far forward on the upper surface of the centrum. From this point the posterior margin of the arch curves strongly to form the anterior boundary of the intervertebral opening. The elongate shape and anterior extent of this opening is in contrast with the situation in the dorsal region of the column where this opening is rounder and considerably smaller.

The transverse processes on vertebrae 2 to 7 show the following gradual changes from the pattern in vertebrae 2: (1) shift to a

higher position on the lateral surface of the neural arch; (2) increased lateral elongation; (3) change of angle of projection of the process from 45 degrees to the sagittal plane in vertebra 2 to almost 90 degrees in vertebra 7; (4) increase in the size of the articular surface with the rib tuberculum and accompanied change in shape to an oval head plus an attached thinner ridge than runs anteroventrally to the anterior centrosphene (there is apparently no gap on the process to separate the oval head from the thinner ridge for the passage of the segmental artery); (5) development of a ridge connecting the prezygapophysis with the dorsal margin of the diapophysis. Similar changes are seen in *Araeoscelis*, but the shift is not as gradual as in *Petrolacosaurus* and occurs between vertebrae 7 and 9.

In response to the greatly elongated centra, the zygapophyses in the cervical region are also unusually elongate and well-developed. Both pre- and postzygapophyses are strengthened by longitudinal ridges. In addition, the prezygapophyses are supported by buttresses directed dorsally and anteriorly. The postzygapophyses are braced above by paired supports descending and diverging posteriorly. These supports, when viewed from the rear, have a convex margin laterally giving the neural arch its slightly swollen appearance. Posteriorly from the third cervical vertebra, the neural arches show a gradual increase in this convexity, which reaches its maximum on the posterior dorsal region. This convexity represents additional bone above the articular surface to withstand the pressure acting on it.

The prezygapophyses of the cervical vertebrae extend far beyond the anterior end of the centra. The postzygapophyses extend only as far as the posterior end of the centra. This is in contrast to the situation in the dorsal region where both zygapophyses extend slightly beyond the ends of the centra.

Both zygapophyses extend far laterally, well beyond the lateral limit of the centrum. The articular surfaces of the zygapophyses are large and are curved transversely. The plane of the articular surfaces is close to the horizontal, but the exact angle cannot be established. Because of the large articular surfaces, the members of each pair of zygapophyses are not widely separated.

The neural spines are situated well toward the posterior end of the vertebrae, centered between the postzygapophyses. Each spine is bordered both anteriorly and posteriorly by paired ridges curving dorsally from each zygapophysis. These ridges continue dorsally for some distance. Between these ridges, the base of the spine shows signs of lateral excavation, but the fossa thus formed does not become really conspicuous until the seventh vertebra. The neural spine of the third cervical vertebra is low in lateral aspect. In dorsal view, the spine is unusually wide and bears two deep longitudinal grooves along the dorsal surface. The neural spines change in shape and gradually increase in height posteriorly along the column. The spine on vertebra 5 is roughly rectangular in lateral aspect and bears a distinct mammillary process on each side. Posterior to the fifth vertebra the neural spines have a pair of mammillary processes; these persist until vertebra 11. The shape of these processes and their position on the neural spine changes along the column: in vertebra 5, the pair of mammillary processes occurs anteriorly, in vertebra 6 it lies about midway along the spine and by vertebra 8 it is near the posterior end. The mammillary processes, which are also seen in *Araeoscelis* and *Prolacerta* probably provided attachment for strong intervertebral muscles or ligaments (Vaughn, 1955; Gow, 1975).

Intercentra in the cervical region are relatively large, well-developed elements; they are up to 1.5 mm long in KUVP 9951 and 33607. The exposed ventral surface bears a well-developed longitudinal ridge; there are no capitular facets at the lateral extremities of the intercentra. Each intercentrum extends far dorsally between the centra.
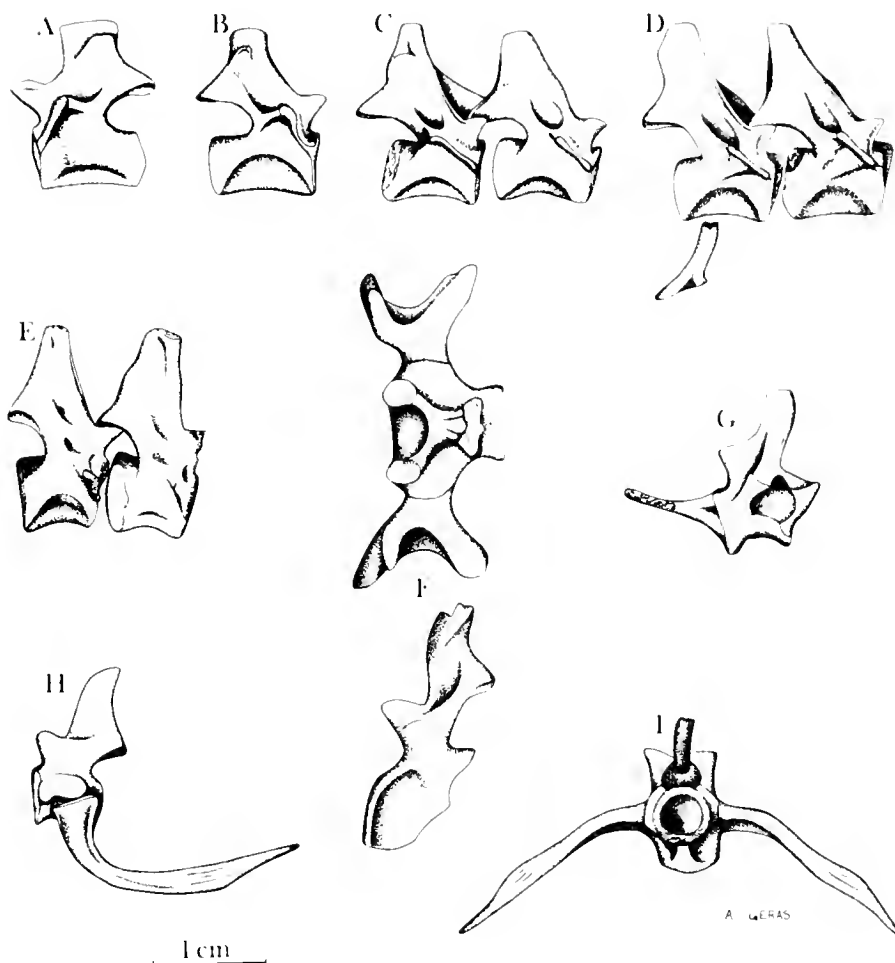
FIG. 15.—*Petrolacosaurus kansensis* Lane. Dorsal, sacral and caudal vertebrae with some associated ribs, all × 1.5. (A-C) Lateral view of vertebrae 7, 8, 13 and 14, KUVP 9951. (D) Lateral view of vertebrae 17 and 18, KUVP 9951. (E) Lateral view of vertebrae 25 and 26, KUVP 33606b. (F) Dorsal and lateral views of first sacral neural arch and ribs, KUVP 33605. (G) Partially preserved second sacral vertebra and rib in anterior view, KUVP 33606b. (H-I) Lateral and anterior views of anterior caudal vertebrae and associated ribs, KUVP 33606c.

DORSAL VERTEBRAE

Dorsal vertebrae (Fig. 15) are considerably shorter than the cervical vertebrae. The centra in KUVP 9951 decrease gradually in length from 9 mm in anterior dorsal vertebrae, to 8 mm in typical mid-dorsals and down to 7 mm in posterior dorsals. The centra in the dorsal vertebrae are stoutly built, with a length to posterior height ratio of 1.3:1 in vertebra 14, in contrast to the condition in the cervical region where the ratio is 2.5:1 (vertebra 3). The absolute height of the centra increases slightly in the dorsal region, and there is bevelling of the ventral surface anteriorly and especially posteriorly to accommodate the intercentra. Intercentral gaps are, therefore, small. Between the anterior and posterior ends of the centrum the lateral surface is strongly concave when viewed in cross-section. The keel, seen in cervical vertebrae, is retained in dorsal vertebrae, but the ventral border of the keel is

broadly rounded as the longitudinal ridge does not descend far ventrally.

The neural arches of the dorsal vertebrae contribute much less to the anterior centrosphene than in cervical vertebrae. The transverse processes in the dorsal region are not only quite different from those in the neck but also undergo considerable change. The transverse processes in the anterior dorsal region have undergone a number of changes from the pattern seen in the posterior cervical vertebrae: (1) the transverse processes have migrated anteriorly onto the prezygapophyses; (2) the lateral elongation of the transverse process has decreased; (3) although the articular surface changes in configuration to correspond to the cross-sectional outline of the head on the dorsal ribs, there is no gap between two oval areas of articulation as there is in *Araeoscelis*, but a single elongate surface of articulation; (4) the transverse process, because of its position on the prezygapophysis, is braced by the same ridges as the latter; (5) in addition, however, a well-developed ridge runs posteromedially from the top of the transverse process to the body of the arch.

Caudad from vertebra 8 the transverse processes gradually decrease both in their lateral projection from the surface of the arch and in the length of the articular surface. By vertebra 20, the articular surface is quite short but still retains both "heads" on the neural arch. Posterior to this vertebra, the articular surface is located further anteroventrally and continues to decrease in size so that by vertebra 23 only the diapophyseal area of attachment is present; it lies close to the centrum near the anterior centrosphene. Presumably the rest of the articular surface for the rib is now part of the centrosphene. In vertebra 26, the tiny articular surface sits on a small knoblike projection at the anteroventral corner of the neural arch as in *Araeoscelis*.

The pre- and postzygapophyses of all dorsal vertebrae extend laterally slightly beyond the centra. The zygapophyseal planes are tilted medially at about 10 degrees to the horizontal. The zygapophyseal surfaces are smaller than in the cervical region.

The neural arches of all the dorsal vertebrae are excavated by deep lateral fossae. The fossae are found by the prezygapophyseal buttress that forms the anterior margin of the neural spine and by the ridge that extends anteroventrally from the postzygapophysis. The fossae are most pronounced on mid-dorsal and posterior dorsal vertebrae. The neural arches are slightly swollen above the postzygapophyses, but only in the dorsal vertebrae.

The gradual increase in neural spine height, noted in the cervical region, continues throughout the anterior dorsal region until vertebra 18. The spines on vertebra 7 to 11 bear short dorsolaterally directed mammillary processes; these are located on the posterior half of the spine, close to the tip. The mammillary processes disappear completely by vertebra 12. In a number of articulated posterior dorsal vertebrae (KUVP 9951, 33605 and 33606), the spines vary in size; every second spine is either somewhat wider anteroposteriorly (KUVP 9951 and 33606) or taller (KUVP 33605) than the intervening one. The function of such alternations in the size of the neural spines is not understood. Similar patterns of neural spine size alternation have been observed by the author in *Captorhinus*, *Eocaptorhinus*, *Araeoscelis* and *Labidosaurus*.

Well-developed intercentra are present throughout the dorsal region of the column. They are about 1.5 mm long in KUVP 9951.

SACRAL VERTEBRAE

Sacral vertebrae are preserved in KUVP 9951, 33605 and 33606. The first sacral vertebra is distinguishable from the posterior dorsal vertebrae by the following features: the two prezygapophyses extend as far laterally as on the dorsal vertebrae, but the postzygapophyses extend only about half as far from the midline. The extremely massive diapophyses extend anterolaterally from high on

the neural arch. The neural spine is inclined posteriorly and has a mammillary-like process (KUVP 33605) on each side at its posterodorsal tip. Anterodorsally, the spine bears two longitudinal grooves along the crest, marking the probable site of the strong interspinous ligament that runs to the last dorsal vertebra.

The centrum is slightly smaller than those of the posterior dorsal vertebrae. Ventral to the diapophysis, but separated from it by a deep groove, is the small longitudinal parapophysis. It lies on the lateral surface of the centrum at the anterior end. The intercentrum does not fuse with the centrum as reported in *Araeoscelis* (Vaughn, 1955) and a number of other Paleozoic reptiles (Romer and Price, 1940).

Less information is available on the second sacral vertebra. The pre- and postzygapophyses conform to the width set by the postzygapophyses of the first sacral vertebra. The anterodorsal edge of the neural spine is also grooved on the second sacral vertebra. This suggests that the first and second sacral vertebrae were also connected by well-developed interspinous ligaments. The neural spine on the second sacral vertebra is considerably smaller than the one on the first. The diapophysis is also smaller, although it is still considerably larger than the processes on the mid-dorsal vertebrae. The distinct diapophysis and parapophysis form the articulation with the rib. No information is available on the second sacral intercentrum or centrum.

Caudal Vertebrae

The anterior caudal vertebrae in *Petrolacosaurus* are somewhat similar to the second sacral vertebra and are considerably altered from the pattern seen in the dorsal series. They are roughly 25 per cent smaller in all dimensions than the mid-dorsals and consequently are less stoutly built. The width of the centrum is slightly greater than the height and is equal to the length. The longitudinal ventral ridge on the centrum does not extend as far ventrally as in the mid-dorsals and its

ventral edge is not as broadly rounded. The lateral excavations above the ridge are not as deep as in the dorsal vertebrae. The zygapophyses are lightly built with considerably smaller zygapophyseal surfaces than in the dorsals. The articular surfaces are tilted at about 25 degrees to the horizontal plane.

The lateral surface of the neural arch of the anterior caudal vertebrae is less deeply excavated than in the dorsal vertebrae. No swelling is apparent on the arch, above the postzygapophyses. The spines are also much smaller and alternation of width is not evident. The transverse process, on the other hand, is more massive than on the dorsal vertebrae and only slightly less well-developed than in the second sacral vertebra. It is difficult to establish whether the diapophysis is distinct from the parapophysis. The incompletely exposed articular surfaces suggest that only one, large, roughly oval surface provides the area of attachment for the rib.

The most anterior caudal intercentra are similar to those of the sacral and presacral vertebrae anterior to them. Posterior to the second caudal vertebra the centra gradually decrease both in width and height, but the length remains relatively constant well into the mid-caudal region. Centra in this region of the vertebral column appear relatively long and laterally compressed. At the fourteenth caudal vertebra, the length to height ratio is 1.8 to 1; by the 39th caudal vertebra, the ratio is 2.2 to 1. Both the ventral longitudinal ridge and the lateral excavation of the centra diminish gradually; by the sixteenth caudal the ventral border of the centrum is gently rounded. The neural arches also diminish gradually in size. The diapophyses disappear by the thirteenth caudal vertebra. The neural spines diminish both in height and lateral extent, disappearing at about the twenty-fourth caudal vertebra. The spines of the anterior and mid-caudal vertebrae follow the general tendency of other primitive reptiles to a slight backward inclination. This posterodorsal inclination increases as the spines decrease both in height and lateral extent pos-

teriorly along the series. Zygapophyses persist beyond the fortieth caudal as simple anterior and posterior projections above the spool-like centra. They are, however, definitely lost by the fiftieth caudal.

Associated with the five anteriormost caudal vertebrae but not preserved in position, are two chevron bones. The first chevron, in KUVP 33606c, probably fits between the third and fourth caudals. As seen in several specimens, they continue posteriorly at least as far as the fortieth caudal vertebra. They are apparently outgrowths of the intercentra and consist of a crescentic intercentral portion, and two thin ventral arms that converge dis-

tally to enclose a vertically elongate foramen. The ventral projection is "Y"-shaped in posterior view. The first chevron appears to be small and delicately built. The second is much larger, with a long ventral projection beyond the foramen. As expected, the chevrons decrease in length posteriorly, albeit gradually.

Ribs

As in all known primitive reptiles, ribs are present on every vertebra from the atlas to, and including, the proximal caudal vertebrae. The head of most ribs includes capitular and tubercular portions, but these vary consider-
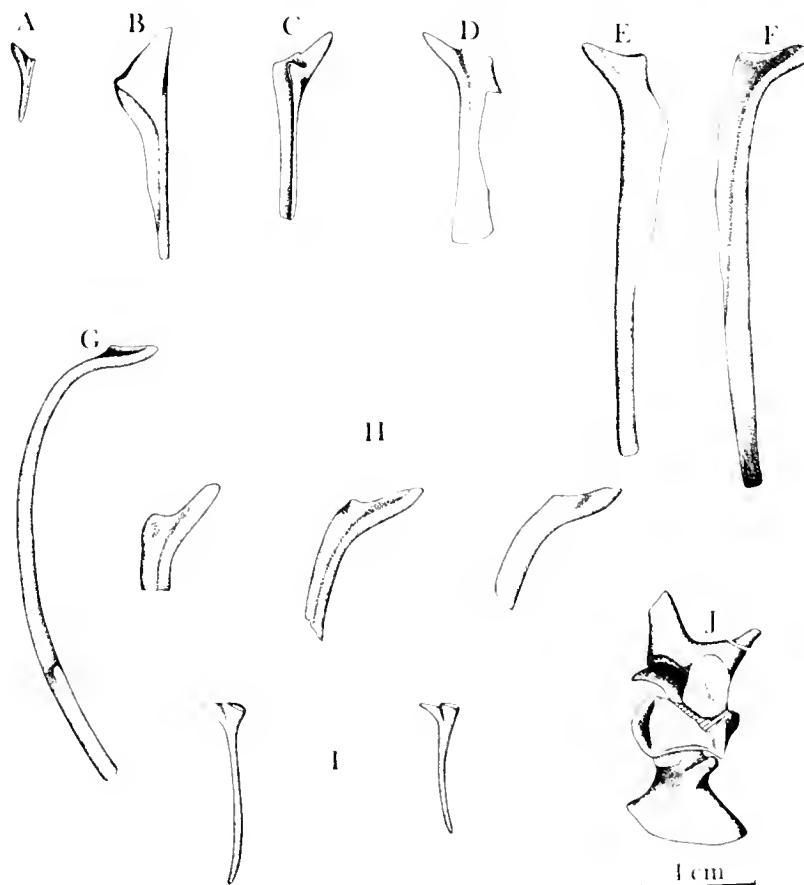
Fig. 16.—*Petrolacosaurus kansensis* Lane. Ribs, all × 1.5. (A-B) Atlantal and axial ribs in lateral view, KUVP 9951 and 33601. (C) Ventrolateral view of fifth rib, KUVP 9956. (D) Medial view of sixth (cervical) rib, KUVP 9956. (E) Medial view of seventh (first dorsal) rib, KUVP 9956. (F) Anterodorsal view of eighth rib, slightly crushed, KUVP 9956. (G) Anterior view of rib 15 slightly crushed, KUVP 9951. (H) Proximal ends of anterior dorsal ribs 9-11, KUVP 9956. (I) Posterior dorsal ribs 23 and 25, KUVP 33606b. (J) Ventral view of first sacral rib and lateral view of first sacral vertebra, KUVP 33606b.

ably along the column both in the degree of their development and in their relation to one another. In the anterior cervical, posterior dorsal and sacral regions, the ribs have distinct gaps between the tubercular and capitular surfaces of articulation for the passage of the segmental artery. Along the rest of the presacral column the rib heads have a single continuous hourglass-shaped area of articulation, with rounded dorsal and ventral margins and a thinner spanning portion. The dorsal and ventral ends of the area of articulation probably correspond to the capitulum and tuberculum of dichocephalous ribs. None of the ribs is immovably fused to the body of the vertebrae.

In the cervical region (Fig. 16) the shafts of the ribs typically run without curving distally from the expanded heads. The atlantal rib (KUVP 33607) is the smallest of the cervical ribs. The tuberculum and capitulum are joined by a thin connecting web. The tuberculum articulated with the atlantal neural arch, while the capitulum reached ventrally to the atlantal intercentrum. Distally from the expanded head, the rib narrows rapidly to a point. The second (axial) and third cervical ribs are each more than twice the size of the first. Although they retain the same structural pattern as the first rib, they do not taper to a point distally. Unlike that of the first three cervicals, the distal end of the fourth, fifth and sixth ribs is flattened and expanded to a paddle-like blade, probably to provide additional support for the levator and serratus musculature that runs to the scapula. The seventh cervical rib is almost twice as long as the sixth, but unlike that of the dorsal ribs, its shaft is nearly straight.

The fourth and fifth cervical ribs have a small anterolaterally directed process close to the anteroventral end of the head. The sixth and seventh ribs have a thin dorsally directed flange, running along the external edge of the shaft. On the sixth this flange runs along most of the length of the shaft, whereas on the seventh it is restricted to the proximal half.

In a typical dorsal rib (Fig. 16), the shaft extends dorsolaterally from the capitulum, whose articular surface is oval in outline and occupies the head of the rib. The tuberculum does not project markedly from the shaft. Its articular surface is also oval in outline and broader distally. The two heads are connected by a narrow web of bone whose edge apposes the corresponding articular surface on the neural arch. Distally from the tuberculum, the rib curves strongly laterally and ventrally. This curvature indicates that the trunk was relatively high and narrow.

Except for the rather flattened promixal end, typical dorsal ribs are oval in section. A small ridge is usually present along the posterodorsal margin. Proceeding posteriorly along the dorsal series, the posterior dorsal ribs as far as rib twenty-one appear to be essentially similar to more anterior dorsal ribs but show a gradual decrease in length and in the size of the head. From the twenty-second rib back, this decrease becomes very pronounced. Rib twenty-three is about half as long as a typical dorsal rib. The shaft is slender and almost straight. The tubercular and capitular heads are separated by a small depression for the passage of the segmental artery. The tuberculum of this rib still attaches to the neural arch. The capitulum, however, attaches to a small facet on the centrum, which is confluent with the anterior centrosphene. Rib twenty-five is still shorter and more slender.

The first sacral rib preserved in KUVP 9951, 9956, 33605 and 33606b consists of a short, massive, cylindrical proximal portion that expands laterally to reach out towards the inner surface of the ilium. Its distal margin is applied to the inner surface of that bone but not fused to it. The first sacral rib articulates with its vertebra, in a large rounded tubercular articulation that begins on the neural arch and passes ventrally onto the centrum. The capitulum is separated from the tuberculum by a small groove and, as in *Araeoscelis* (Vaughn, 1955) extends anteroventrally to attach to the intercentrum. Beyond the articular area, the neck of the rib

narrows slightly, then abruptly flares laterally as a cupped expansion that widens below, and is bounded anteriorly and posteriorly by two heavy ridges. Between these ridges the rib is strongly concave with its lateral surface almost vertical. The rib terminates laterally in a broad, roughly "U"-shaped strongly curved border, which articulates with a corresponding groove on the ilium.

The second sacral rib is much more slender than the first. The smaller tuberculum and capitulum articulate with the neural arch and centrum respectively. The shaft of this rib extends as far laterally as the first, but its distal expansion against the ilium is less pronounced. Its distal end, as in *Araeoscelis* (Vaughn, 1955), has a dual function: bracing the posterior end of the first rib from below and articulating with the ilium.

The caudal ribs are markedly different in character from those preceding them. They extend laterally, curve slightly forward, then turn sharply posteriorly in a horizontal plane. The proximal part of each rib in KUVP 33606c has a longitudinal groove on the ventral surface, reflecting the probable dichocephalous character of the head, yet examination of the proximal surface of the rib reveals no distinct tubercular and capitular surfaces for attachment to the vertebra. A single, oval surface serves this function. The shaft of the rib is circular in section. Posteriorly the rib tapers to a pointed tip. The first and second caudal ribs are unusual in having a laterally directed portion of the rib. This flange bears longitudinal ridges, probably for muscle attachment.

The anterior caudal ribs are elongate. The first of the series reaches far beyond the posterior end of the corresponding vertebra. Succeeding ribs run posteriorly parallel to, and medial to the first. They diminish rapidly in length and disappear by the eleventh or twelfth caudal vertebra.

PECTORAL GIRDLE

The first description of the shoulder girdle of *Petrolacosaurus* was based on an immature specimen, KUVP 1427 (Peabody, 1952, Fig. 2). The study of much better material, belonging to mature individuals in KUVP 9957, 33606 and 33607 indicates that Peabody's left scapulocoracoid is in fact an incompletely preserved scapula with no trace of either anterior or posterior coracoids. In addition, the elements tentatively identified as the cleithrum and clavicle are quite different from the well preserved, complete cleithrum in KUVP 33607 and clavicles in KUVP 9958 and 33606. They may, in fact, be interpreted as isolated lower jaw elements since a splenial lies nearby.

Cleithrum.—The cleithrum in KUVP 33607 (Figs. 12 and 13) is a long, narrow bone with a slightly expanded head, quite similar in general proportions to that found in Pennsylvanian captorhinomorphs (Carroll and Baird, 1972). The head consists of an oval plate that was probably applied to the anterior end of the cartilaginous extrascapula. Its outer surface is only slightly sculptured. The slender shaft is flattened. The medial surface of the bone is strongly grooved to receive the anterior margin of the scapula. The lower end appears to have overlapped the clavicle. The M. levator scapulae inferioris presumably attached to the well developed ridge that runs along the anterior margin of the cleithrum (Holmes, 1977).

Clavicle.—The clavicle in KUVP 33606, found in close association with the skull and other postcranial elements, is exposed in medial view. A second, isolated clavicle belonging to a juvenile individual is exposed in lateral view (KUVP 9958, Fig. 17c). The clavicle consists of a narrow dorsal process and an expanded plate. The outer surface of the dorsal process shows two grooved areas. Near the upper end, the anterior margin of the clavicle is longitudinally striated to receive the overlapping lower end of the cleithrum. The whole of the posterior margin of the shaft is strongly grooved to receive the anterior edge of the scapula. At the end of the shaft the external lip of the groove broadens posteriorly and conceals the groove from
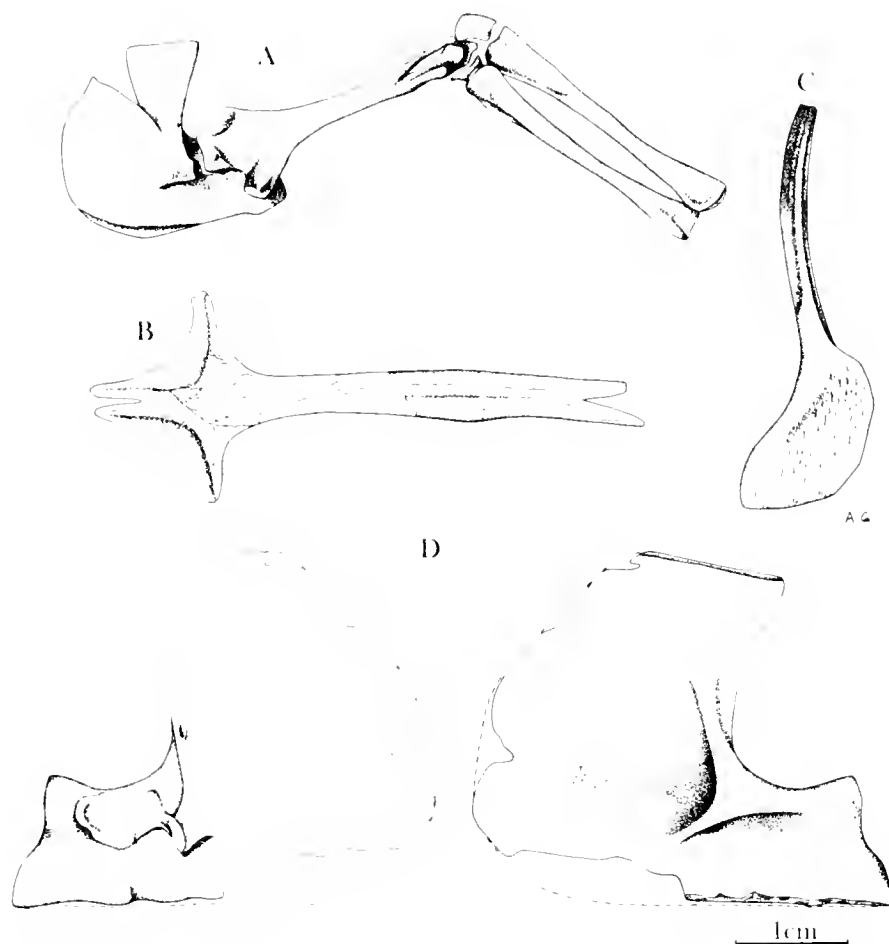
FIG. 17.—*Petrolacosaurus kansensis* Lane. Pectoral girdle. (A) Lateral view of left scapulacoracoid in articulation with limb, KUVP 9957a, × 0.75. (B) Ventral view of slightly immature interclavicle, KUVP 9959b, × 1.5. (C) Lateral view of left clavicle, immature, KUVP 9958, × 1.5. (D) Lateral and medial views of right scapulacoracoid, KUVP 33609, × 2. See Figs. 12 and 13 for cleithrum.

lateral view. The narrow dorsal process of the clavicle probably provided excellent attachment for the clavicular portion of the deltoid and trapezius muscles. The plate-like portion of the clavicle is relatively massive in comparison to that in primitive captorhinomorphs, but is comparable to the clavicle of *Araeoscelis* (Vaughn, 1955). This plate is inflected medially on the shaft at an angle of about 45 degrees. The expansion of this portion of the clavicle is formed largely by a strong anterior curvature of the thickened anterior margin. The lower portion of the clavicle has striations running to the ventro-medial margin. The ventromedial margin is gently convex. It appears that the clavicles covered the anterior part of the head of the interclavicle head but did not meet at the midline.

Interclavicle.—The isolated, immature, interclavicle found in KUVP 9959b has a diamond-shaped head and a long stem (Fig. 17b). The exposed ventral surface of the head is strongly convex. The greater part of the head is depressed, bears no sculpturing, and lies internal to the clavicles. This isolated element has been associated with *Petrolacosaurus* partly because the depressed areas

on the head correspond closely in outline to
the medial end of the clavicular blade. In
addition, the raised portion of the head, which
forms the posterior quarter of the diamond
and extends anteriorly between the clavicles,
bears the distinctive type of sculpturing seen
on the clavicle and the dermal skull roof
elements. The stem of the interclavicle is a
flat straight blade that runs along the ventral
midline of the pectoral girdle. It lies on the
external surface of the bony scapulacoracoid
and the unossified sternum. The ventral sur-
face of the blade is missing in KUVP 9959b,
except for the posterior third, where a series
of bilaterally arranged longitudinal grooves is
seen. The anterior and posterior tips of the
bone bifurcate.

Scapulocoracoid. — The scapulocoracoid
(Fig. 17d) is present in four adult specimens,
KUVP 9957a, 33606c, 33607 and 33609, and
appears to be ossified as a unit with no su-
tures separating the anterior and posterior
coracoids and scapula. The only indication
of a division between the anterior and pos-
terior coracoids is a delicate crack that runs
dorsoventrally through the glenoid cavity in
the right scapulacoracoid of KUVP 9957a. In
immature specimens, however, the component
elements show postmortem separation.

In general proportions the scapulocoracoid
resembles those of the primitive captorhino-
morph *Protorothyris archeri* (Clark and Car-
roll, 1973, Fig. 6) and *Araeoscelis* (Vaughn,
1955) except that the scapular blade in *Petro-
lacosaurus* is much wider. The straight dorsal
margin of the scapula is unfinished, indicating
that the endochondral girdle continued dor-
sally in cartilage. The anterior portion of the
blade is very thin transversely. The posterior
margin of the scapula curves posterodorsally
as in *Araeoscelis*. Ventrally this margin is
continued as two ridges. One forms the pos-
terior boundary of the supraglenoid buttress
and extends posteriorly onto the posterior
coracoid. A second, more prominent ridge
extends straight down to the massive anterior
glenoid buttress and forms the anterior boun-
dary of the triangular supraglenoid buttress.

As in *Paleothyris* and *Protorothyris* the supra-
glenoid foramen opens externally on this
second ridge, just above the tip of the supra-
glenoid buttress.

The glenoid cavity has the usual screw-
shape seen in most early tetrapods (Romer,
1956; Holmes, 1977). The anterior part of
the glenoid projects far laterally, supported
by the massive anterior glenoid buttress. The
external opening of the coracoid foramen lies
within a deep pocket, beneath this buttress.
Behind the glenoid there is a prominent proc-
ess for the origin of the coracoid head of the
triceps muscle. This structure, common in
pelycosaurs, is also found in *Protorothyris* and
Araeoscelis. The large external surface of the
anterior coracoid area is smoothly confluent
with that of the scapular blade. Close to the
ventral margin, the external surface of the
coracoids is unfinished.

The medial surface of the right scapulo-
coracoid in KUVP 33609 closely resembles
that of *Protorothyris* (Clark and Carroll,
1973). A system of two ridges has the outline
of an inverted "T." One of these ridges
extends vertically onto the scapular area me-
dial to the supraglenoid buttress. The second
diverges anteriorly and posteriorly from the
base of the first and supports the anteroven-
tral part of the anterior coracoid and the
glenoid respectively. In contrast to the con-
dition in *Protorothyris*, where there are two
internal openings of the supraglenoid fora-
men, there is only a single internal opening in
Petrolacosaurus, in the upper part of the deep
subcoracoscapular fossa. The coracoid fora-
men probably opened into the lower part of
the subcoracoscapular fossa, as in other early
reptiles, but this area of the fossa is slightly
damaged in KUVP 33609.

PELVIC GIRDLE

Both Lane (1945) and Peabody (1952)
based their description of the pelvic girdle on
the isolated left half of a pelvis (KUVP 1425)
that is definitely that of an edaphosaurian
pelycosaur. There is now conclusive evidence
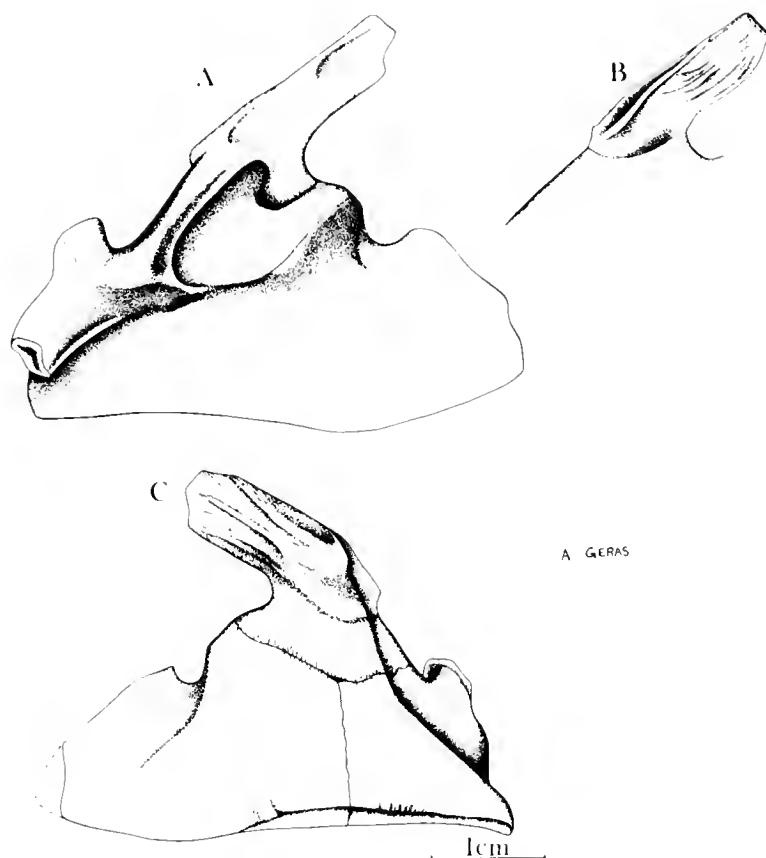that this element does not belong to *Petrola-*

FIG. 18.—*Petrolacosaurus kansensis* Lane. Pelvic girdle, × 1.5. (A) Lateral view of slightly crushed left pelvis, KUVP 9961. (B) Medial view of right iliac blade, uncrushed, KUVP 33606c. (C) Medial view of slightly crushed left pelvis, KUVP 9951.

cosaurus. In KUVP 33606 part of the left side of a mature pelvis, exposed in medial view, is closely associated with a series of posterior dorsal, sacral and anterior caudal vertebrae, on a small block which also contains other remains of *Petrolacosaurus.* In KUVP 9951c the complete pelvis, exposed in lateral and medial views, is closely associated with both hindlimbs and lies near a series of articulated presacral vertebrae and a scattered skull of the same genus. These pelves are unique in several features and can be readily distinguished from those of other Paleozoic reptiles. The pelvis mistakenly ascribed by Lane and Peabody to *Petrolacosaurus* probably pertains to *Edaphosaurus* sp.

which has also been found in the Garnett quarry.

In its general proportions and in the structure of the component elements, the pelvic girdle (Fig. 18) resembles that of *Araeoscelis* more closely than the girdle of any other reptile, but also retains a number of primitive features seen in primitive captorhinomorphs. In contrast to the pectoral girdle, which in *Petrolacosaurus* is lightly built and is ossified as a unit in mature individuals, the pelvic girdle is massive and the sutures between the component elements are always easily discernible in medial view. The acetabular cavity is primitive in its configuration, with the three raised corners of the cavity supported by prominent buttresses on each of the three

pelvic elements. In both KUVP 9951 and 9961 the unfinished articular surface of the acetabulum extends to the posterior margin of the pelvis, as in *Araeoscelis* (Vaughn, 1955).

Ilium.—The ilium has a long blade which extends far posterodorsally and only slightly anteriorly. This condition, also seen in all captorhinomorphs, *Araeoscelis* and ophiacodont pelycosaurs, is considered primitive. The posterior end of the blade in *Petrolacosaurus* is thin in cross-section, and its lower corner tends to have been lost during preservation.

The internal surface of the ilium, superbly preserved in KUVP 33606c, is more significant than the lateral. Near the dorsal edge a well developed shelf of bone extends medially along much of the length of the iliac blade. This process, not found in captorhinomorphs, is well developed in *Araeoscelis* (Vaughn, 1955), and in ophiacodont pelycosaurs. The central region of the medial iliac surface is slightly recessed and rugose below the medially directed shelf to receive the sacral ribs. Neither of these structural features of the internal surface of the ilium are found in captorhinomorphs. The posterior half of the medial surface of the blade shows a series of longitudinal ridges, similar to those seen in the primitive captorhinomorph *Coelostegus* (Carroll and Baird, 1972, Fig. 14) for the origin of epaxial musculature.

Pubis.—The pubis, well preserved in both KUVP 9951c and 9961 is massively built. As in *Araeoscelis*, the anterolateral margin is formed by a thick ridge that is a continuation of the anterior iliac ridge. A large tubercle projects dorsolaterally from this ridge. Its function, according to Vaughn (1955) was to raise the anteroventral end of the iliopubic ligament in the absence of a well developed anterior expansion of the iliac blade. This tubercle is also found in *Paleothyris* and in primitive ophiacodonts, but in these genera is much smaller than in either *Petrolacosaurus* or *Araeoscelis*. A second, smaller process extends ventrolaterally from the ridge connecting the lateral pubic tubercle to the acetabulum. This process, also seen in *Araeoscelis*,

probably served as the origin for the ambiens and pubotibialis muscles. The true pubic tubercle, located at the distal end of the ridge is also massive. As in other early reptiles the pubic part of the puboischiadic plate faces more or less ventrally and is not fully seen in lateral view. The external opening of the obturator foramen, which is much larger than in primitive captorhinomorphs, lies directly beneath the anterior end of the acetabulum. On the internal surface of the pubis, the unfinished symphysial surface is relatively narrow, running along the ventromedial margin. The internal opening of the obturator foramen is obscured in all the preserved specimens, but probably lies on the upper part of the large pubic surface which faces not only dorsomedially but also anteriorly.

Ischium.—The ischium in *Petrolacosaurus* is the most distinctive element of the pelvis. In captorhinomorphs and pelycosaurs the long dorsal margin of the ischium is strengthened by a rounded ridge. No such ischiadic ridge is found here. Posterior to the acetabulum, the thin dorsal margin of the ischium is deeply notched, a feature unique to *Petrolacosaurus*. The posterior margin of the notch flares dorsolaterally. Posterior to the notch the margin of the ischium remains thin and curves medially to the posteromedial corner of the bone. The M. ischiotrochantericus apparently passed from the posteromedial surface of the ischium laterally ventral to the ilioischiadic ligament to insert onto the proximal end of the femur. The dorsolateral flare of the ischiadic notch probably served as the attachment area for a shortened and hence stronger, ilio-ischiadic ligament. The notch itself likely served as a lateral passage for M. ischiotrochantericus. On the internal ischiadic surface a ridge extending posteromedially from the notch, roughly parallel to the posterior margin, limits the area of origin of the above muscle. This posterior area of the ischium is slightly offset from the general internal surface. No such specialization is seen in any other early reptile.
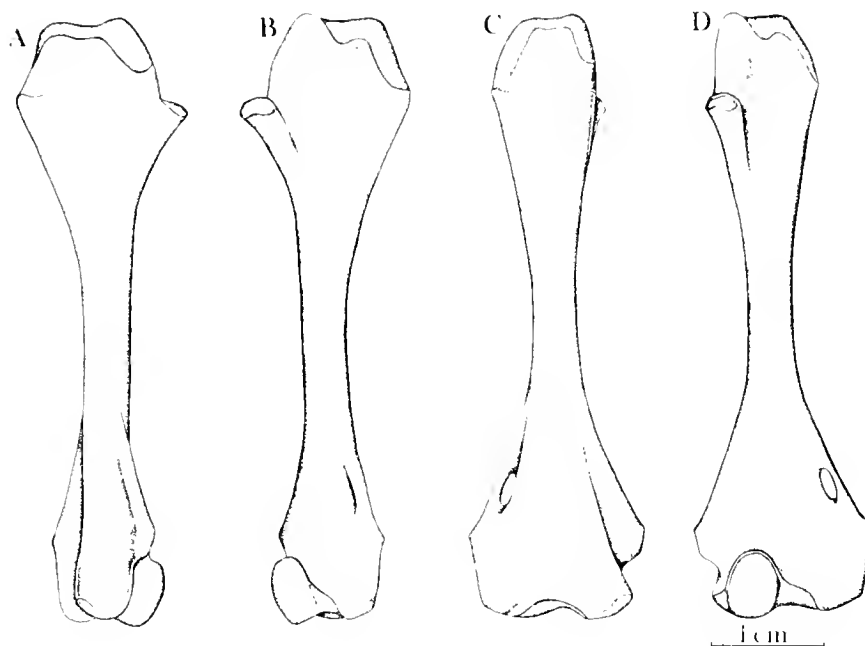
FIG. 19.—*Petrolacosaurus kansensis* Lane. Reconstruction of the right humerus, × 1.5. (A-D) Proximal dorsal, proximal ventral, distal dorsal and distal ventral surfaces, based mainly on KUVP 9957 and 33606a.

LIMBS

A total of twenty-six limbs, belonging to fourteen individuals have been recovered. Most of these were originally complete as they lay in the matrix. Only eight were completely isolated from the body. Of the limbs associated with the girdles, only one was in articulation (KUVP 9957a, Fig. 17).

Humerus.—The reconstruction of the humerus (Fig. 19) is based mainly on two mature but crushed bones, found in KUVP 9957a and 33606a. The humerus is of the tetrahedral type common to primitive reptiles (Holmes, 1977) but the shaft is better developed than in primitive captorhinomorphs and pelycosaurs. The width of the proximal end of the humerus forms about 27 per cent of the length of the bone, and the distal width is about 29 per cent of the length. The shaft is exceedingly slender, only about 7 per cent of the length. These proportions are comparable to those found in *Araeoscelis* (Vaughn, 1955).

The estimated twist of the distal upon the proximal plane is 60 degrees. Following Romer and Price's (1940) terminology, the humeral surfaces in *Petrolacosaurus* can be divided into proximal dorsal, distal dorsal, proximal ventral and distal ventral surfaces.

The proximal dorsal surface was probably gently convex along the long axis of the bone. Severe crushing flattened the proximal head. The surface shows a distinct ridge for the M. latissimus dorsi. A long narrow ridge for the M. deltoideus insertion runs distally from the delto-pectoral crest.

The proximal ventral surface was probably deeply concave below the articular surface. The M. coracobrachialis brevis inserted in the concave region. The anterior proximal area, above the delto-pectoral crest, is rounded and lacks any rugosity. In modern lizards, the M. supracoracoideus inserts on this area (Holmes, 1977). Distally, a distinct delto-pectoral crest juts out anteroventrally from the proximal head. At the summit of this crest is a relatively small circular area with a rugose surface to which attached the powerful pec-

toralis musculature. Distally, the crest slopes rapidly into the shaft; its internal border sends a delicate ridge distally to the entepicondyle.

A well-developed entepicondylar foramen and a large supinator process distinguish the distal head of the humerus of *Petrolacosaurus* from that of most pelycosaurs (Romer and Price, 1940) as well as from *Araeoscelis*. The radial nerve was only partially surrounded by bone as it traversed the humerus, whereas in *Araeoscelis* it was fully enclosed in bone (ectepicondylar foramen).

The entepicondyle does not extend far laterally. Its rugose lateral and distal margin furnished the areas of origin of the flexor musculature of the lower arm and foot. The inferior humeral nerve apparently ran along the deep groove on the dorsal surface of the entepicondyle, passed through the elongate entepicondylar foramen, and entered the forearm, as in *Sphenodon* (Miner, 1925). On the distal dorsal surface, the entepicondyle is separated from the ectepicondyle by a long groove that widens distally. The moderately developed ectepicondyle is a long ridge that widens as it runs distally. Its end projects distally above and beyond the general contours of the humerus. Its rugose distal head furnished a small area for the origin of much of the extensor musculature of the lower arm and foot. Anteriorly the ectepicondyle is bounded by the long ectepicondylar groove. In pelycosaurs the entepicondyle is usually larger and the ectepicondyle projects further dorsally than in *Petrolacosaurus* (Romer and Price, 1940).

Anterior to the deep ectepicondylar groove, which carried the radial nerve, the supinator process lies below the level of the ectepicondyle and the general dorsal surface. Unlike that in pelycosaurs, the supinator process in *Petrolacosaurus* does not project strongly outward but extends far distally. Its rugose tip lies close to the distal end of the bone and probably furnished a small area for the origin of the supinator muscles. The fully
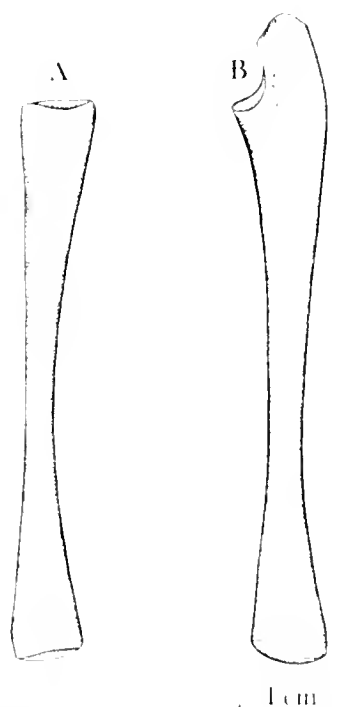

Fig. 20.—*Petrolacosaurus kansensis* Lane. Left radius (A) and ulna (B) in dorsal (preaxial) view, KUVP 9957, × 2.

enclosed ectepicondylar foramen in *Araeo-scelis* extended the possible area of origin of the supinator musculature, as in modern lizards (Romer, 1944). A ligament, running from the supinator process to the ectepicondyle in *Petrolacosaurus*, may have served the same function.

The lateral edges of the distal ventral surface are formed by the margins of the entepicondyle and the supinator process. Between these margins the ventral surface is relatively flat but is pierced by the oval entepicondylar foramen. Much of the distal end of the humerus is occupied by the radial and ulnar articulations. The radial articulation (capitellum) is a slightly elongate swelling with an unfinished surface. The capitellum not only projects ventrally but also slightly distally, suggesting that the epipodials met the longitudinal humeral plane at an obtuse angle. The capitellum is contiguous with the ulnar articulation posterior to it. The concave surface of the latter faces essentially distally. Proximally from the articular area, the ventral surface is slightly depressed.

Radius.—The radius (Fig. 20) is a long, slender element with slightly expanded ends. In the articulated left forelimb of KUVP 9957a (Fig. 17) the length of the radius is .92 per cent of the length of the humerus. The width of the proximal end measures about 14 per cent of the length of the bone and the distal width about 12 per cent of the length. The proximal head is cup-shaped for the humeral articulation. Because of crushing, its outline cannot be determined. The lateral and medial edges of the bone, seen in anterior view, are partially formed by two longitudinal ridges that probably separated the extensor and flexor muscles. The medial ridge is quite prominent proximally and is slightly rugose. The distal head of the radius is turned slightly laterally so that the autopodial surface can be seen in lateral view.

Ulna.—The ulna (Fig. 20) is also quite long and slender; it is slightly longer than the humerus. The maximum width of the proximal end approaches 15 per cent of the length

of the element, whereas the distal end is narrower—about 12 per cent of the length. The shaft, as in the radius, narrows to 5 per cent of the length of the bone. The ulna has a well developed olecranon and a concave sigmoid notch for articulation with the humerus. The tip of the olecranon is capped by a ridge that curves over the apex of the bone. The main tendon of the triceps musculature probably attached here. The sigmoid notch occupies the whole thickness of the medial side of the head. The articular surface is highly curved, turning through an arc of about 140 degrees, while the distal end of the notch faces proximally, its proximal end faces medially and slightly distally. The anterior surface near the humeral articulation is rugose. The anterior and posterior surfaces are separated medially by a rounded ridge. The distal end of the ulna is expanded and is twisted slightly laterally. The autopodial surface is convex.

Femur.—The reconstruction of the femur (Fig. 22) is based on the holotype KUVP 1424, as well as on KUVP 9951d and 33606. Dorsoventral crushing has flattened the femora and bent the internal trochanter. This prevents consideration of the femur in anterior and posterior views. The femur is closely comparable to that of primitive captorhinomorphs and pelycosaurs. It is more massive than the femur in *Araeoscelis* (Vaughn, 1955).

The width of both the proximal and distal ends of the bone is about 30 per cent of the length. The relatively massive shaft narrows to about 13 per cent of the length.

The proximal head of the femur is terminal as in all primitive reptiles and not inflected medially. The articular surface is crescentic. The anterior portion of the articular area is the broadest. Distal to the head, a prominent anterior crest extends onto the ventral surface of the femur. The crest's proximal end probably forms the internal trochanter for the tendinous insertion of the M. puboischiofemoralis externus. The distal extension of the crest along the shaft forms a
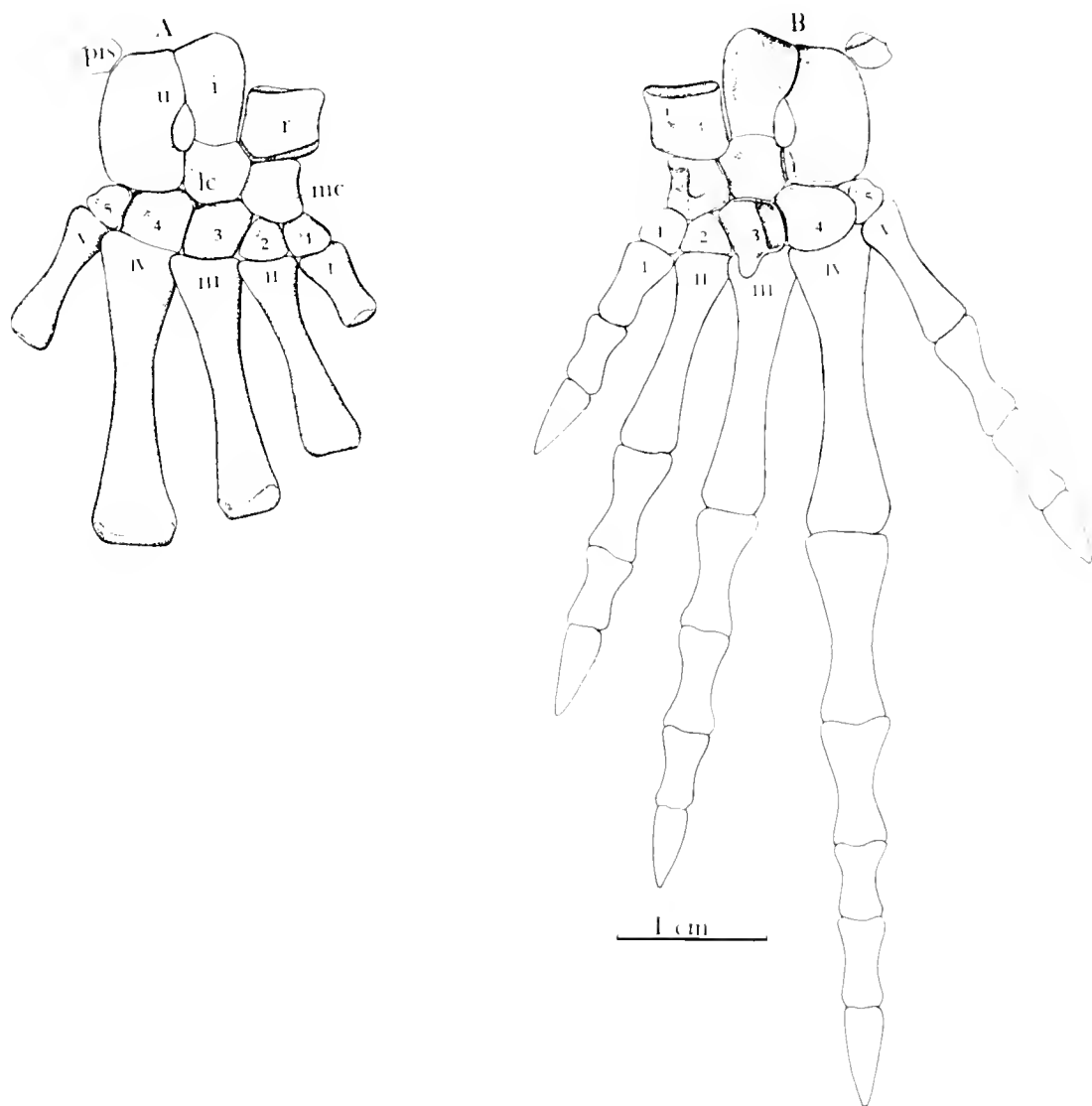
Fig. 21.—*Petrolocasaurus kansensis* Lane. Reconstruction of the right manus in dorsal (A) and ventral (B) views, based mainly in KUVP 1423, 8355 and 9957b, × 2.0. Abbreviations used in this Figure: i, intermedium; lc, lateral centrale; mc, medial centrale; pis, pisiform; r, radiale; u, ulnare; 1-5, distal carpals; I-V, metacarpals.

linea aspera for the insertion of the adductor musculature. There is no distinct fourth trochanter. The ventral surface of the proximal head is occupied by the deeply hollowed intertrochanteric fossa for the M. puboischiofemoralis externus.

In dorsal view, the proximal head has a smoothly curved, conical surface broken posteriorly by a well developed tuberosity ap-

parently for the probable insertion of the M. ischiotrochantericus. The smooth, curved, dorsal surface extends distally onto the broad shaft. Two prominent ridges on the dorsal surface of the distal head run proximally from the articular area of the anterior and posterior condyles respectively. The extensor musculature of the lower leg attached to these longitudinal ridges. Beyond these areas of muscle
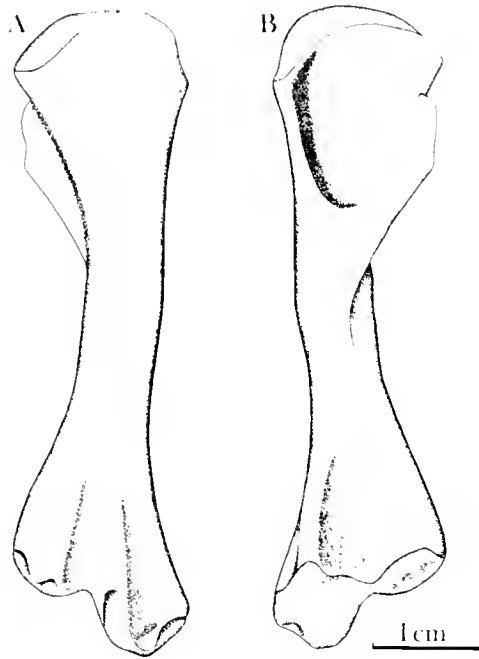
FIG. 22.—*Petrolacosaurus kansensis* Lane. Reconstruction of the left femur in dorsal (A) and ventral (B) views, based mainly on KUVP 9951 and 33606, × 1.5.

attachment, the dorsal condylar surfaces are concave. Between these ridges the femur is notched dorsally by a deep intercondylar fossa for the tendon of the quadriceps muscle. The surfaces for articulation with the tibia and fibula extend onto the dorsal surface.

The distal ventral surface of the femur is deeply concave and rugose. A prominent posterior ridge extends distally along the posterior condyle. Its continuation onto the articular area forms the boundary between the areas of articulation with the tibia and fibula.

Tibia.—The tibia and fibula are known in at least two specimens—KUVP 9951b and 33606. The tibia (Fig. 23) is quite long, its length equalling that of the femur. As with other distal limb bones, the tibia is slender. The width of the head in one specimen is about 20 per cent of the length of the bone, and the distal width is nearly 12 per cent of the length. The shaft has a minimum diameter of only 5.5 per cent of its length. These proportions are comparable to those in *Araeoscelis* (Vaughn, 1955).

The tibia is immediately identifiable by the conspicuous anterior concavity of the shaft and by the large head. The articular surface of the head is similar in outline to that of primitive captorhinomorphs (Carroll, 1969) and pelycosaurs (Romer and Price, 1940). The proximal portion of the tibia is roughly triangular in cross-section as is the outline of the articular surface. Two well developed ridges pass distally along the lateral and anterior margins. The latter probably afforded attachment for an interosseous ligament. As in *Araeoscelis* the distal articular surface of the tibia can be divided into two parts that form a firm, locked joint with the astragalus (Vaughn, 1955).

Fibula.—The fibula (Fig. 23) is very long and slender. The width of the head in a well ossified specimen is about 10 per cent of the length of the bone; the distal width about 15 per cent of the length. These proportions are also comparable to those in *Araeoscelis* (Vaughn, 1955). The fibula in *Petrolacosaurus* is rather blade-like, with prominent
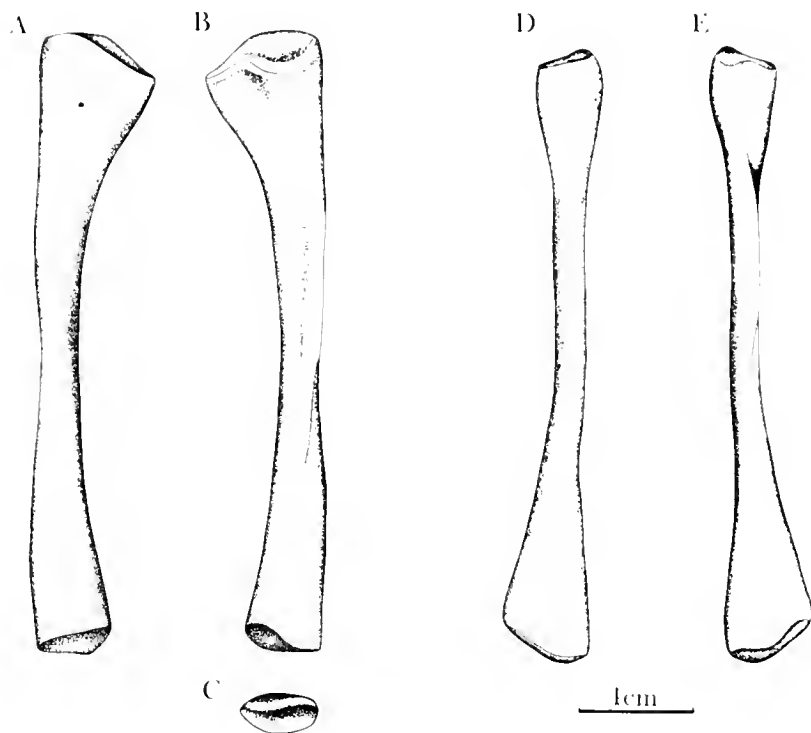
Fig. 23.—*Petrolacosaurus kansensis* Lane. Tibia and fibula, × 1.5. (A-B) Dorsal and ventral views of the left tibia in KUVP 9951. (C) Distal articular surface of (B). (D-E) Dorsal and ventral views of the left fibula in KUVP 9951.

medial and lateral ridges. The medial ridge for the interosseous ligament is blade-like. The medial margin of the fibula, formed by the above ridge, is slightly concave. The proximal portion of the fibula is somewhat twisted in relation to the distal one. The proximal articulatory surface for the femur is key-hole shaped, due to crushing. The distal surface, on the other hand, is elongate and divided into distinct astragalar and calcaneular areas.

Manus.—The manus is well represented by eight specimens. Nearly all features of the manus are seen in both dorsal and ventral views. The general number and arrangement of bones resembles closely that of captorhinomorphs. The preserved carpal bones are either in perfect articulation, or only slightly disarticulated. All the elements are well ossified with fully developed articulating surfaces. They appear to have fitted com-

pactly together to form a well knit structure with little cartilage between articular surfaces (Fig. 21).

In general proportions, the carpus in *Petrolacosaurus* is similar to that in *Araeoscelis* (Vaughn, 1955). It is slightly more elongate than the carpus in primitive captorhinomorphs (Carroll and Baird, 1972). This elongation is probably related to the elongation of the radius and ulna. The ulnare is the largest element of the carpus, is attached proximally to the ulna and the small pisiform, and is supported distally by the fourth and fifth distal carpals. It varies in outline from a discoid in KUVP 8355 to a highly elongate structure in KUVP 33606, equal in length to an anterior dorsal vertebra. It is possible to account for this variation by the apparent immaturity of the former specimen. The ulnare of the mature individual, seen in KUVP 33607 is a massive element, braced by a pair of

ridges near the medial edge. The more prominent of the two ridges extends on the dorsal surface between the proximal and distal articular surfaces. A similar, but smaller, ridge exposed in KUVP 9957b, extends proximodistally on the ventral surface. Both the proximal and distal articulatory surfaces are contiguous with a pair of unusually massive medially and ventromedially directed facets that articulate with the intermedium and medial centrale respectively. Between these facets, the medial margin of the bone is deeply notched to form the lateral surface of the perforating foramen.

The intermedium in *Petrolacosaurus* is also an elongate element, although it is shorter than the ulnare. In KUVP 33607 the intermedium is two-thirds the length of the ulnare. The surface of the proximal articulation with the ulna is continuous with a massive medial articular surface with the ulnare. This surface, exposed in both KUVP 9957b and 33607, faces somewhat ventrally. The small, oval distal articulation of the intermedium is restricted to the lateral centrale, as in *Araeoscelis* (Vaughn, 1955) and pelycosaurs (Romer and Price, 1940), rather than being supported by both the lateral centrale and ulnare, as in *Paleothyris* (Carroll, 1969). A well developed ridge extends proximodistally along the lateral edge of the intermedium. Between the articular surfaces with the lunare and the lateral centrale, the intermedium forms the rounded medial surface of the perforating foramen. The medial edge of the intermedium is thin and is free of contact with the radiale.

The radiale, best preserved in KUVP 8355 is a short, massive element supported by both the medial and lateral centrale. As in *Araeoscelis* and numerous other early reptiles the radiale in *Petrolacosaurus* bears a longitudinal ridge on its dorsal surface. On the ventral surface, this element has a pronounced proximal depression, which is interrupted by a proximally directed ridge. The radial surface is nearly transverse to the long axis, as in *Araeoscelis* (Vaughn, 1955) rather than being

strongly tilted dorsally as in many pelycosaurs (Romer and Price, 1940). The bulbous distal articular surface fits into the angle formed by the centralia.

The lateral centrale in *Petrolacosaurus* is a relatively short element which has contacts with most of the other carpal bones. In addition to supporting the three proximal carpal elements, it also articulates with the medial centrale and the third and fourth distal carpals. Between the ventrolaterally directed process for articulation to the ulnare and the proximal articulation to the intermedium, the medial centrale contributes to the margin of the perforating foramen. The dorsal surface of the lateral centrale also bears a prominent longitudinal ridge. Whereas in primitive captorhinomorphs (Carroll, 1969) and pelycosaurs (Romer and Price, 1940) the lateral centrale is elongate and the medial centrale is short and broad, in *Petrolacosaurus* the two centralia are similar in shape.

The medial centrale is similar in shape to that in *Araeoscelis* (Vaughn, 1955). It supports proximally much of the weight of the radiale and articulates distally not only with the first and second distal carpals but also with a portion of the third. Its ventral surface, exposed in KUVP 9957b bears a prominent finger-like process that extends towards the first distal carpal.

The fourth distal carpal, as in other early reptiles, is the largest of the series, and bears most of the support of the ulnare. Medially it does contribute to the support of the lateral centrale. The ventral surface of the fourth distal carpal is considerably larger than the dorsal and overlaps much of the head of the fourth metacarpal and a portion of the small triangular fifth distal carpal. The third distal carpal supports most of the weight of the lateral centrale and part of the medial centrale. It is only slightly smaller than the third, at least in dorsal view. In KUVP 9957b the third distal carpal is exposed in both dorsal and ventral views. The ventral surface of this element is considerably smaller than its dorsal surface because the large surface of

articulation with the fourth distal carpal faces ventrolaterally. In addition to this unusual feature, the third distal carpal also has a prominent finger-like process that extends distally beneath the head of the third metacarpal, well beyond the carpal-metacarpal articulation. The finger-like processes on the ventral surface of the third distal carpal and the medial centrale and the ridge on the radiale may have provided attachment areas for the flexor musculature of the forelimb.

The first and second distal carpals support the medial centrale and are comparable in size to the fifth.

A complete set of metacarpals occurs in perfect articulation with the rest of the immature forelimb in KUVP 1423 (Peabody, 1952, Fig. 6c). These metacarpals show a range in length from 4 mm (first) to 14.5 mm (fourth). The proximal heads overlap one another, as in *Araeoscelis* (Vaughn, 1955) and many diapsids (Carroll, 1975), restricting considerably independent metacarpal movement. Such metacarpal overlap is not found in captorhinids (Holmes, 1977). As indicated by Peabody (1952, pp. 28 and 29) both metacarpals and phalanges are relatively long and slender, as in other small early reptiles. The phalangeal count is 2, 3, 4, 5, 3. The terminal phalanges are developed into long, sharp claws, similar to those found in primitive captorhinomorphs and early pelycosaurs.

One of the most striking features of the manus in *Petrolacosaurus* relates to the orientation of the articular surfaces between the ulnare and intermedium, between the ulnare and lateral centrale, and between the third and fourth distals. The ventral edges of these surfaces are widely separated if the carpus is reconstructed as a completely flattened structure (Fig. 21). This indicates that in life *Petrolacosaurus* had a strongly curved carpus, with a medio-laterally convex dorsal surface. Most of this curvature was formed along the long axis of the carpus. The extent of this curvature cannot be established with certainty, however, because of crushing. The type of carpal curvature seen in *Petrolaco-*

saurus has not been found in any other Paleozoic reptile. This may, however, be due to the general lack of information about the ventral aspect of the carpus in early reptiles.

A definite joint plane is lacking within the carpus, and even between the carpus and the paired distal limb elements. Movement between the carpus and the metacarpals apparently was also slight because the proximal heads of the metatarsals overlap one another, the line between the carpals and metacarpals is curved, not straight, and the distal ends of the third and fourth distal carpals restricted the downward movement of the corresponding metacarpals considerably. It is probable, therefore, that bending during locomotion was achieved by discreet accommodation throughout the manus.

Pes.—The pes is almost completely articulated in the type specimen KUVP 1424 (Peabody, 1952, Fig. 9), but most of the bone is gone, leaving an impression on the matrix. The interpretation of the tarsus given here (Fig. 24) is based on well preserved left and right tarsi, exposed in both dorsal and ventral views (KUVP 9951a and b) and a partial right tarsus (KUVP 33606) from mature individuals. Peabody suggested that the first tarsal bone was lost in *Petrolacosaurus*. This element is, however, present in both the left and right tarsi on KUVP 9951a and b. The general arrangement of the tarsal elements resembles that of *Araeoscelis* (Vaughn, 1955) and to a lesser extent that of the primitive captorhinomorph *Paleothyris* (Carroll, 1969). The shape and level of ossification of the component elements indicates that the pes was a compact structure, as was the mature manus.

The astragalus is the most distinctive element in the tarsus. It is a long, relatively slender bone. As in other primitive reptiles it is essentially "L"-shaped, with a distinct neck region, the proximal end of which forms part of the tarso-fibular articulation. The dorsal surface of the astragalus, exposed in KUVP 9951b, is gently concave. The lateral border of the astragalus forms a massive

articulation with the calcaneum along the length of the bone, interrupted only near the distal end by a small notch that forms the medial border of the perforating foramen. This longitudinal articular surface faces dorsally, in part, in KUVP 9951b suggesting that the pes, like the manus, is curved transversely but with a concave dorsal surface. The laterodistal corner of the astragalus bears a condyloid process, similar to that in *Araeoscelis* (Vaughn, 1955), which articulates with the calcaneum laterally and to the fourth tarsal distally. The distal border of the astragalus is notched between the condyloid corner and the articulation with the centrale. In contrast to the condition in captorhinomorphs and pelycosaurus, where the tibial surface on the astragalus is convex, that of *Petrolacosaurus* (as it is exposed in medial view in KUVP 33606) is strongly concave, with two massive ridges, separated by a trough. One of these ridges forms the thickened distal two-thirds of the medial border. The second prominent ridge located on the ventral surface runs roughly parallel to the lateral border. This arrangement of a pair of ridges separated by a deep trough is also seen in *Araeoscelis* and in the eosuchian *Kenyasaurus* (Harris and Carroll, 1977). The distal articular surface of the tibia is divided into a lateral trough and a medial ridge, which fits snugly onto the astragalus to form a firm, locked joint. On the ventral surface of the astragalus a strong ridge connects the distal lip of a deep fossa, which extends to the perforating foramen, with the proximal end of the tibial surface. A notch in the distal border, exposed in dorsal view, extends onto the ventral surface as a small fossa which receives the latero-proximal end of the centrale.

The calcaneum in *Petrolacosaurus* is a relatively simple oval structure with a thick medial portion that supports the proximal fibular facet and the distal tarsal articulation. A somewhat thinner plate extends laterally. Both dorsal and ventral surfaces are gently concave. The straight medial margin, which articulates with the astragalus, is interrupted

by the small notch that forms the lateral margin of the perforating foramen. The broad, rounded distal border of the calcaneum apposes the fourth and fifth distal tarsals. An unfinished area, marking the area of articulation with the distal tarsals, extends far onto the ventral surface of the calcaneum. Except for this extended area of articulation there is nothing to distinguish this calcaneum from those of pelycosaurs.

In contrast to the condition in primitive pelycosaurs, where there are both lateral and medial centralia in the pes (Romer and Price, 1940), there is only a single large centrale in *Petrolacosaurus* and most captorhinomorphs. It supported the astragalus. This element, completely preserved in KUVP 9951a and b, is much compressed proximodistally. It articulates with the rounded distomedial surface of the astragalus. The proximal articular surface of the centrale is deeply concave, whereas the distal surface for articulation with the first three distal tarsals and the lateral surface for articulation with the fourth distal tarsal are strongly convex. Both dorsal and ventral surfaces of the centrale show a central depression bound proximally by the ridged margin of the bone.

All the distal tarsals are well preserved in KUVP 9951a and b and only slightly disarticulated from one another. As in other early reptiles, the fourth distal tarsal is the largest of the series and bears much of the weight of both the astragalus and calcaneum. The dorsal and ventral surfaces are gently concave. The dorsal surface of this bone is contiguous distally with the broadly convex articular surface for the fourth metatarsal. All other articular surfaces of the fourth tarsal are sharply offset from both the dorsal and ventral surfaces. Medially the fourth distal tarsal articulates with the centrale and the third distal tarsal by a complicated system of concave and convex surfaces (Fig. 24). The proximal articular surface is strongly concave. Laterally the fourth distal tarsal articulates with the fifth distal by an extensive dorsolaterally inclined surface. The first distal tarsal is also

deeply concave proximally in *Petrolacosaurus* and matches the length of the fourth. The lateral surface of the fifth distal tarsal is smoothly continuous with the narrow distal surface, and is unfinished. This indicates that both these surfaces articulated with the large head of the fifth metatarsal. The fifth metatarsal was, therefore, widely divergent.

The third distal tarsal not only has relatively small, simple, dorsal and ventral surfaces, but also has extensive and complicated articular surfaces with the centrale and the second and fourth distal tarsals. The first and

second distal tarsals, like the third, have larger lateral and medial surfaces than either the dorsally or ventrally exposed areas.

The articular surfaces between the proximal and distal elements of the tarsus extend in a straight line roughly perpendicular to the long axis of the pes; in addition, the proximal surface, formed by the astragalus and calcaneum has a rounded, strongly convex outline and fits into the strongly concave distal articular surface formed by the centrale and the fourth and fifth distal tarsals. The configuration of the mesotarsal articulation indicates,
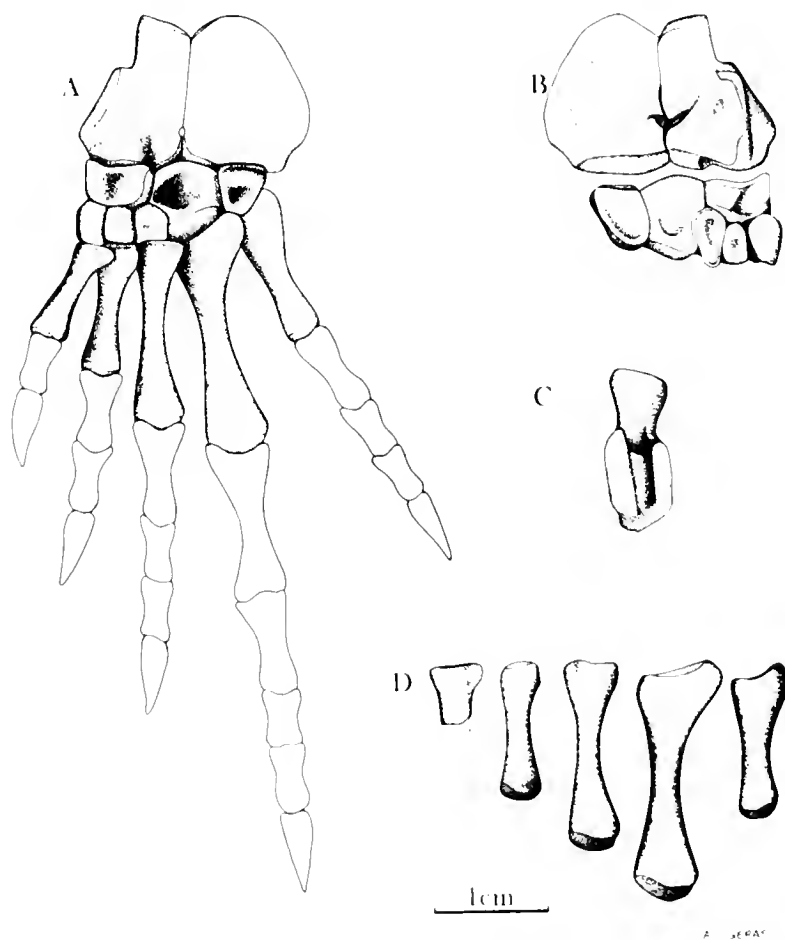
Fig. 21. *Petrolacosaurus kansensis* Lane. Pes, all × 1.5. (A) Reconstruction of the left pes, in dorsal view, based mainly on KUVP 1424 and 9951b. (B) Ventral view of the left tarsus, restored with the mesotarsal surfaces exposed, KUVP 9951a. (C) Medial view of the right astragalus, KUVP 33606. (D) Metatarsals in dorsal view, KUVP 9951b. Abbreviations used in this Figure: as, astragalus; cal, calcaneum; cp, centralia pedis; fib, articulation with fibula; tib, articulation with tibia; 1-5, distal tarsals; I-V, metatarsals.

therefore, that hinge movement between the proximal and distal elements is probable, while the distal elements are solidly attached to one another with little possible movement between them. Similarly, in primitive capto-rhinomorphs and pelycosaurs, a functional mesotarsal joint may have been present, but the corresponding articular surfaces are not as well adapted to movement as in *Petrolacosaurus*.

The metatarsals in general resemble the metacarpals, except that the fourth and fifth metatarsals have large proximal ends. The heads of both of these metatarsals have strongly ridged medial portions and slender lateral portions which also extend proximally. The proximal articular surfaces are not perpendicular to the long axis of the metatarsal. The proximal ends engage each other in characteristic overlap. This overlap is, however, more accentuated in the pes than in the manus.

The phalangeal count, based upon the type specimen is 2, 3, 4, 5, 4. The terminal phalanges are modified into claws similar to those in *Paleothyris*.

PHYLOGENETIC RELATIONSHIPS
OF *PETROLACOSAURUS*

In the first detailed study of *Petrolacosaurus* Peabody (1952) tried to establish the probable relationships of this animal by comparing it with reptiliomorph "amphibians" (diadectids and seymouriamorphs), captorhinomorph reptiles, pelycosaurian reptiles and diapsid reptiles. He separated those morphological features of *Petrolacosaurus* that are also found in many amphibians (shared primitive characters, or symplesiomorphies of Hennig) from those he believed were "progressive features" present in captorhinomorphs or pelycosaurs or eosuchians (shared derived characters, or synapomorphies of Hennig). His conclusion that *Petrolacosaurus* is an eosuchian diapsid reptile rather than a pelycosaur and that it is close to the primary dichotomy of the reptilian radiation was generally rejected (Stovall, Price and Romer, 1966). The reasons for this rejection are two fold. The fossil material available to Peabody for study was meager and crucial portions of the skull and postcranial skeleton were unknown. In his analysis of relationships Peabody included among his "progressive features" many morphological characters that later proved to be characteristics of early reptiliomorph amphibians or all early reptiles, rather than features restricted to particular reptilian taxa. For example the suture pattern of the palate in *Petrolacosaurus* is close to that of *Youngina*, as indicated by Peabody (1952) but is also similar to the pattern seen in primitive captorhinomorphs (Carroll and Baird, 1972), pelycosaurs, millerosaurs (Gow, 1972) and even such reptiliomorph amphibians as *Gephyrostegus* (Carroll, 1970) and *Limnoscelis* (Heaton, in press). The discovery and study of nearly complete, well preserved specimens of *Petrolacosaurus* and recent studies of other Paleozoic reptiles (Carroll, 1964, 1969; Carroll and Baird, 1972; Clark and Carroll, 1973; Gow, 1972, 1975; Heaton, 1979; Holmes, 1977;

Reisz, 1972; Vaughn, 1955) provide a strong basis for the critical evaluation of the phylogenetic relationships of this unique early reptile.

For the purposes of this discussion strict monophyly for the Amniota is assumed. It is further assumed that the following groups of late Paleozoic and early Mesozoic fossils can be included within the Amniota: pareiasaurs, procolophonians, millerosaurs, mesosaurs, pelycosaurs, captorhinomorphs and "eosuchians." In order to test rigorously hypotheses of relationships of the Petrolacosauridae some well-tested equivalent level phylogenetic system is needed within the Amniota, but this is not available. No restricted outgroups can be developed either; only an unresolved multichotomy containing at least four of the above seven groups. It was therefore felt that the following procedure should be pursued: Those characters shared by most of the above early reptiles will be considered shared primitive characters (symplesiomorphs) for Amniota and removed from discussion when testing hypotheses of relationships of *Petrolacosaurus*. These characters are listed below and separated from later discussions because retention in *Petrolacosaurus* of many of these primitive characters does not in itself indicate close phylogenetic relationships within the Amniota (Hennig, 1966). Hypotheses of relationships of *Petrolacosaurus* will be then presented, the basic taxa discussed and the hypotheses tested using shared derived characters.

PRIMITIVE CHARACTERS

(1) While pelycosaurs show exponential increase in size during the Pennsylvanian, protorothyridids, "eosuchians," millerosaurs, mesosaurs and procolophonids retain almost the same body size throughout their history (Reisz, 1972). Among the protorothyridids

the skull also increases in length only slightly (Table I). The skull of the largest known specimen of *Petrolacosaurus* is only slightly longer than the skull of the largest known protorothyridid, *Protorothyris archeri*.

The outline of the skull in dorsal view resembles an isosceles triangle with a rounded apex and with sides that bulge out slightly, close to the base. In captorhinids, the skull becomes bulkier and wider than in protorothyridids. Among pelycosaurs a great variety of skull outlines exists from the slender, elongate skulls seen in ophiacodonts to the bulky, wide configuration of edaphosaurs and caseids.

The skull profile remains relatively low. The maximum skull width is greater than the maximum height in any transverse section of the skull roof. The ventral edge of the cheek is nearly straight from the snout to the suspensorium. The posterior edge of the skull is tilted only slightly forward. In advanced pelycosaurs, on the other hand, the skull profile deepens in the temporal region and the ventral edge of the cheek is often strongly curved ventrally.

The outline of the skull in protorothyridids, millerosaurs, "eosuchians" and *Petrolacosaurus*, in occipital view, resembles a trapezoid with rounded upper angles. The nature of preservation of most primitive reptiles precludes precise determination of the angle between the cheek and the skull table. It is only slightly greater than 100 degrees in the captorhinomorph *Protorothyris*, and similar estimates have been computed for *Paleothyris* on the basis of the width of the palate and skull table (Carroll and Baird, 1972). The wealth of material available for the reconstruction of *Petrolacosaurus* shows an angle of 100 ± 5 degrees. A more precise determination of this angle was not possible because of the curvature of both the cheek and skull table. In pelycosaurs other than caseids and eothyridids the occiput is much higher than in either protorothyridids, eosuchians, millerosaurs, or *Petrolacosaurus*.

(2) The interrelationship of the bones of the cheeks, skull table, palate, occiput and mandible remains relatively constant in millerosaurs, protorothyridids and primitive pelycosaurs (Gow, 1972; Romer and Price, 1940; Reisz, in press). Most features of this pattern are retained in the skull of *Petrolacosaurus* in spite of the morphological advances associated with cranial fenestration.

The dorsal expansion of the maxilla remains moderate in most early reptiles. The long lacrimal extends from the external naris to the orbit, and forms a large portion of the anterior orbital margin. Although *Petrolacosaurus*, most captorhinomorphs, millerosaurs and primitive pelycosaurs retain this condition, in more advanced pelycosaurs, "eosuchians" and mesosaurs the lacrimal fails to reach the external naris because of the dorsal expansion of the maxilla. In most early reptiles the jugal forms part of the ventral margin of the cheek. The squamosal and the quadratojugal form the slightly convex posterior margin of the cheek. The postorbital extends to the supratemporal. The supratemporal bone is large in parieasaurs, procolophonians, millerosaurs and primitive pelycosaurs. In ventral view, the occipital condyle extends posteriorly to the level of the jaw suspension. In protorothyridids, millerosaurs, pelycosaurs, "eosuchians" and *Petrolacosaurus*, the long pterygoids are wedged anteriorly between the vomers. Three rows of well-developed palatal teeth radiate from the basipterygoid area in most early reptiles; the largest palatal teeth are present on the transverse flange of the pterygoid. The long, relatively narrow palatine abutts anteriorly against the plate-like vomer that forms most of the medial margin of the internal naris. The ectopterygoid is small. The parasphenoid is denticulate.

The paired postparietal and tabular bones are restricted to the occiput. The occipital condyle is located far ventrally on the occiput, close to the level of the jaw articulation. A large subvertical strip of the squamosal extends onto the occiput. The posterior edge of the dorsal process of the quadrate is cov-
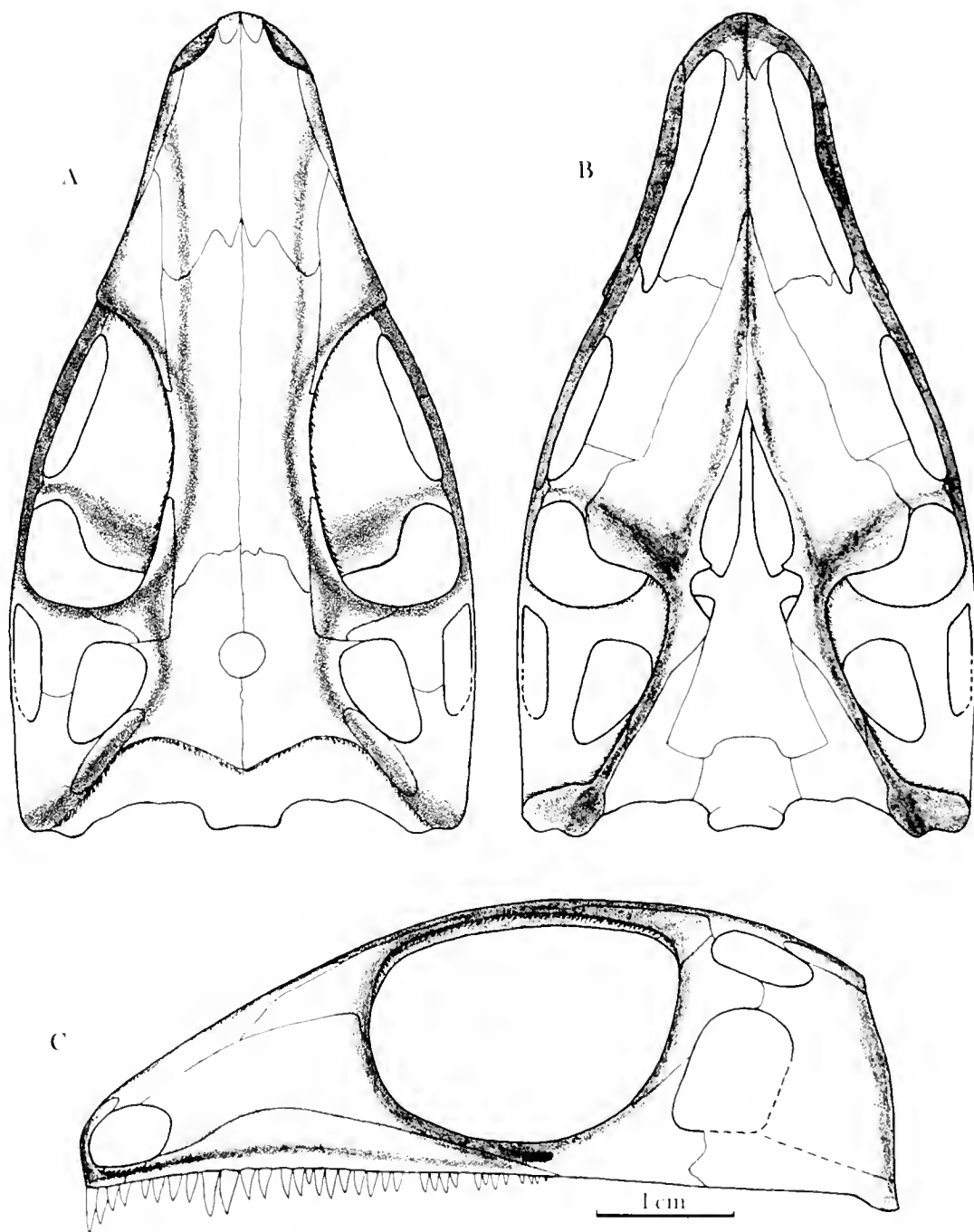
FIG. 25.—*Petrolacosaurus kansensis* Lane. Pattern of internal cranial ridges or thickenings in (A) dorsal, (B) ventral and (C) lateral views, × 2. Composite. See text for further explanation.

ered by it, except in the region of the quadrate foramen. The dorsal process of the quadrate is inclined slightly anterodorsally. In mesosaurs, early "eosuchians," captorhinomorphs, pelycosaurs, procolophonids there is no otic notch. The stapes is massive and has both a dorsal process and a footplate.

The mandible is long and slender. The coronoid region is little expanded. There is no retroarticular process.

(3) In most early reptiles the marginal teeth are arranged in a single row. They are simple conical structures, slightly recurved, with subthecodont implantation. An anterior food trap is partially associated with some caniniform tooth development.

(4) Vertebrae are amphicoelous and notochordal. Relatively large intercentra are continued in the tail as chevron bones. The atlantal intercentrum is very large, has a well-developed ventral median ridge, and a pair of articular facets for the capitulum of the atlantal rib. In most pelycosaurs, in millerosaurs, "eosuchians" and captorhinomorphs the atlantal centrum is excluded from the ventral border of the column by the axis intercentrum. In *Hylonomus*, the earliest representative of the captorhinomorphs, the atlantal centrum is crescentic in outline and open ventrally. The axial intercentrum is longer than those in the rest of the column. In *Petrolacosaurus* the large axial intercentrum is ventral to the crescentic atlantal centrum and is loosely attached to it. Although these elements are disarticulated in *Hylonomus* [BM(NH)R. 4168], their relative position was apparently similar. In all later captorhinomorphs, however, the axial intercentrum and atlantal centrum are indistinguishably fused. The axial neural arch of *Petrolacosaurus* is strongly built, and has a large spine that extends anteriorly over the atlas, as in the captorhinomorphs, "eosuchians," millerosaurs and pelycosaurs.

The cervical ribs have flattened, slightly expanded ends. The sacral and anterior caudal ribs are firmly attached to the vertebrae. There are two sacral ribs.

The primitive reptilian configuration of the girdles in early captorhinomorphs, millerosaurs and some pelycosaurs is also seen in *Petrolacosaurus*.

The limbs are well ossified. Both proximal and distal limb elements have thick shafts and broad ends. The humerus has a well developed entepicondylar foramen and a supinator process. The manus and pes are relatively large and broad, with a long-necked astragalus and a plate-like calcaneum.

HYPOTHESES OF RELATIONSHIPS

Two of the hypotheses presented and tested here are illustrated in Fig. 26. The first hypothesis is that *Petrolacosaurus* shares a
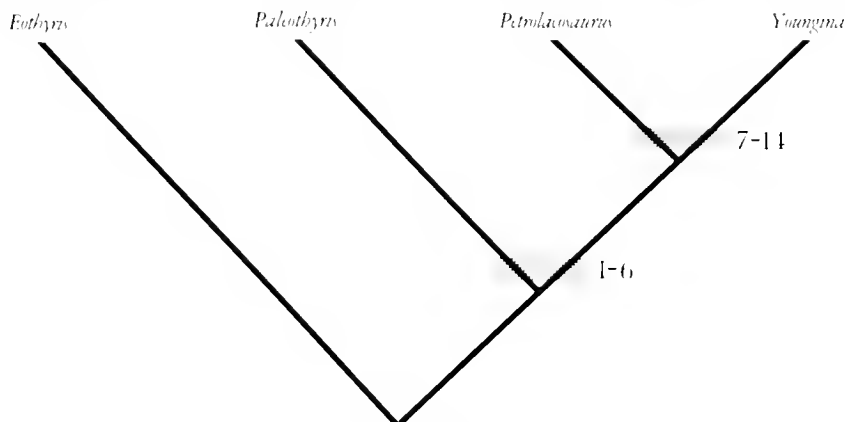

FIG. 26.—Cladogram illustrating hypotheses of relationships of *Petrolacosaurus*. See text for further explanation.

more recent ancestor with the captorhino-morph *Paleothyris* than with the synapsid *Eothyris*. All synapsids could have been used but *Eothyris* was selected as the representa-tive of this group because it is the most primitive pelycosaur and is most similar to *Paleothyris* and protorothyridids. This hy-pothesis is tested by characters 1-6 (see dis-cussion below). The only morphological char-acter that may falsify this hypothesis is the presence of the lower temporal fenestrae in both *Eothyris* and *Petrolacosaurus*. Other significant differences in the architecture of the skulls of these reptiles and the presence of six shared derived characters in the un-fenestrated *Paleothyris* and *Petrolacosaurus* suggest that the lower temporal fenestrae in the above taxa are not phylogenetically ho-mologous.

The second hypothesis is that the primi-tive diapsid *Youngina* shares a more recent ancestor with *Petrolacosaurus* than with the protorothyridid *Paleothyris*. All protorothyri-dids could have been used as the outgroup for the tested characters but *Paleothyris* was selected because it is the most primitive, well preserved protorothyridid, is most similar to *Petrolacosaurus* and is therefore best suited for the search of characters unique to diap-sids. *Youngina* was chosen for comparison with *Petrolacosaurus* because it is the best known early "eosuchian" diapsid reptile (Gow, 1972; Carroll, 1977) and is closest morphologically to the latter species. In addi-tion, there is little evidence to indicate that the "Eosuchia" are strictly monophyletic. Although only *Youngina* is shown in the clad-ogram (Fig. 26), characters 7-14 (see discus-sion below) also test the hypothesis of a monophyletic Diapsida including *Petrolaco-saurus*. No characters are known that falsify this hypothesis.

BASIC TAXA

Eothyris is a small, remarkably primitive, pelycosaur known from a single skull from the Lower Permian of Texas. The family

Eothyrididae, erected as a provisional group by Romer and Price (1940), also included the fragmentary remains of three pelycosaurs of large size because they are "Ophiacodont pelycosaurs, primitive in most known regards but paralleling the higher sphenacodonts in the development of much enlarged canines and showing a tendency toward elongation of the vertebral column" (Romer and Price, 1940, pp. 246-247). Both the presence of caniniform teeth and long vertebrae represent primitive conditions for amniotes, and the dental and vertebral patterns seen in the advanced ophiacodont *Ophiacodon* are de-rived conditions. Both *Stereophallodon* and *Stercorhachis* are ophiacodont pelycosaurs that have retained the primitive dental and vertebral pattern and have been therefore included into the family Ophiacodontidae (Reisz, in press). *Baldwinonus trux* appears to present a more difficult taxonomic problem because the type specimen includes fragments of large ophiacodont vertebrae and the maxilla of a large sphenacodont pelycosaur (pers. obs.). The study of this material is now in progress, but it is certain that none of the materials associated with this species is an eothyridid pelycosaur.

Langston, in his 1965 description of another small eothyridid *Oedaleops campi*, indicated that this species is remarkably simi-lar to *Eothyris*. *Oedaleops* has smaller canini-form teeth than *Eothyris*, similar in size to those found in early captorhinomorphs, but *Oedaleops* is peculiar in that the supratem-poral projects slightly beyond the posterior edge of the cheek. The exact configuration of the posterior end of the supratemporal in *Eothyris* is not known because of overprepa-ration. This posterior projection of the supra-temporal may represent a shared derived character for the family, but further materials are needed before this can be verified.

Eothyridids, represented only by the spe-cies *Eothyris parkeyi* and *Oedaleops campi*, are closely related to the caseid pelycosaurs as indicated by a series of shared derived characters (Reisz, in press). Significant

shared primitive characters found in both caseids and eothyridids that appear in a derived form in all other pelycosaurs are worth noting: The width of the skull is greater than the height, even in the region of the snout; the frontal either does not extend to the orbit (*Eothyris*) or the orbital margin of the frontal is very short (*Oedaleops* and all caseids); the supratemporal bone is large and broad. In captorhinomorphs, millerosaurs and procolophonids the skull retains the primitive cotylosaur pattern of a low-profile skull. This primitive condition persists only in caseid and eothyridid pelycosaurs. In other pelycosaurs, the snout in the edaphosaurs, and the whole skull in ophiacodonts, varanopsids and sphenacodonts becomes narrow and deep. Only in cotylosaurs (*Limnoscelis*, *Diadectes*, *Seymouria*) and the caseid and eothyridid pelycosaurs is the primitive pattern of the frontal retained. In other pelycosaurs, in millerosaurs, and in early captorhinomorphs one-third of the dorsal orbital margin is formed by the frontal. The broad supratemporal, a primitive reptilian and cotylosaurian character is modified in captorhinomorphs, diapsids and advanced pelycosaurs, but persists as a broad sheet in caseids and eothyridids.

Paleothyris, the best known protorothyridid captorhinomorph, was described by Carroll (1969). This small reptile is represented by two nearly complete skeletons and numerous disarticulated specimens, all recovered from a single Middle Pennsylvanian *Sigillaria* stump from Florence, Nova Scotia. *Paleothyris* exhibits a combination of morphological characters that make it the least specialized well preserved member of the family Protorothyrididae. The group of small reptiles placed within this family is characterized by the possession of features usually considered primitive (plesiomorphic) for the Amniota. It is in fact difficult to find any derived characters that are unique to this group. The reasons for this are that (1) no attempt has been made to search for morphological characters that are unique to this group, (2) the placement of the species within the family

was based on solely primitive ("ancestral") characters, and (3) the osteology of most species is based on single partially preserved specimens, or several poorly preserved scattered skeletons. Of the better known protorothyridids, *Cephalerpeton ventriarmatum* (Carroll and Baird, 1972) is specialized in having only 16 large maxillary teeth while *Anthracodromeus longipes* is specialized in having long limbs. The most significant specialization of *Coelostegus prothales* is seen in the skull roof, where the posterior margin is deeply embayed. The Lower Permian *Protorothyris archeri* (Clark and Carroll, 1973) has an unusually large skull and tall neural spines. These species probably represent separate monophyletic taxa rather than a single monophyletic group, but better preserved materials are needed before such an hypothesis can be tested.

A series of diapsids from the later Permian and early Triassic are placed on the basis of primitive characters, within the order "Eosuchia." They are small, and most are poorly known. The assigned genera appear to constitute a number of distinct lineages. The main stock is represented by *Youngina* from the Upper Permian *Daptocephalus* zone of South Africa. This species is known from several skulls described by Broom (1914), Olson (1936), Gow (1975) and Carroll (1977) and from postcranial skeletons described by Broom (1924), Watson (1957) and Gow (1975). The skull of *Youngina* is in many significant features similar to that of *Petrolacosaurus*, including large upper temporal, lower temporal, post-temporal and suborbital fenestrae. There is no otic notch, but the posterior margin of the quadrate is not covered by the squamosal. The vertebrae are quite primitive and close to the pattern seen in captorhinomorphs, but they also have slightly swollen neural arches and powerful zygapophyses, with nearly horizontal articulating surfaces, as seen in *Petrolacosaurus*.

Heleosaurus (Broom, 1907; Carroll, 1976a) from the *Cistecephalus* zone, is known from a single partially preserved specimen appar-

ently combining primitive "eosuchian" features with a number of highly specialized, and possibly archosaurian, adaptations. In this specimen only the palate, marginal bones of the cheek region, lower jaws, an articulated series of presacral vertebrae and ribs, dermal armour-plates along the vertebral column, incomplete girdles and femora are preserved. The known parts of the skull of *Heleosaurus* are similar to the corresponding parts in *Petrolacosaurus* and *Youngina* despite the thecodont marginal dentition. *Heleosaurus* also resembles *Petrolacocaurus* in a number of postcranial features including elongated cervical vertebrae with long prezygapophyses, tilted centrospheres, mammillary processes on the neural spines and well-developed ventral keels. According to Carroll (1976a) the femur in *Heleosaurus* is far advanced from the primitive reptilian configuration, in correlation with an upright posture. Careful examination of the specimen reveals, however, that the exposed posterior surface of the femur was mistakenly identified by Carroll as the ventral surface. The exposed surfaces of both the proximal and distal heads and the curvature of the femur correspond closely to those of primitive captorhinomorphs and is not specialized in the manner suggested by Carroll.

Another genus from the *Cistecephalus* zone, *Galesphyrus*, was originally described by Broom (1915) as a therapsid, but its "eosuchian" nature has since been recognized by Romer (1966) and Carroll (1976b). Although this small reptile is known only from two incomplete postcranial skeletons it has been associated with the "Eosuchia" on the basis of general similarities in size and proportions to *Youngina*, and the particular similarities of the vertebral, carpal and tarsal structures. Many of these morphological characters are also seen in *Petrolacosaurus*.

The postcranial skeleton of a new "eosuchian" reptile, *Kenyasaurus*, from the Triassic beds near Mombasa, Kenya has been described by Harris and Carroll (1977). The type specimen of *Kenyasaurus* has a series of articulated vertebrae that extend from the posterior end of the pectoral girdle to the tip of a long tail. Crushing makes interpretation of the trunk vertebrae difficult, but it appears that, as in *Petrolacosaurus*, the neural arches are massively built, the zygapophyses extend far laterally and the articular surfaces for the ribs in the anterior dorsal region are elongate with expanded dorsal and ventral ends. Although the preserved appendicular skeleton of *Kenyasaurus* is in some features similar to that of *Petrolacosaurus*, the forelimb is specialized in having a wide paddle-like humerus and the fifth tarsal appears to have fused to the fourth tarsal.

A number of primitive, but apparently distinct aquatic eosuchians from the Lower Triassic of Tanzania and Madagascar are currently being described by Mr. Philip J. Currie at the Provincial Museum of Alberta, Edmonton. The early descriptions by Haughton (1924) and Piveteau (1926) reveal little detail, but show general postcranial proportions similar to those noted in *Petrolacosaurus*.

Prolacerta (Camp, 1945; Gow, 1975) from the Lower Triassic *Lystrosaurus* zone of South Africa represents yet another "eosuchian" lineage. Although the skull of *Prolacerta* has an unusual combination of lizard-like and thecodont-like features, it also shares a large number of primitive characters with *Youngina* and *Petrolacosaurus*. There is a well developed upper temporal fenestra, but the lower temporal bar is absent. Although there is an otic notch formed by the quadrate, the squamosal extends far ventrally, preventing streptostyly. Well developed post-temporal and suborbital fenestrae are also present. The dentition is apparently thecodont (Gow, 1975), although the anterior and posterior edges of the teeth are not serrated. The postcranial skeleton of *Prolacerta* is surprisingly similar to that of *Petrolacosaurus*. The atlas-axis complex and the other cervical vertebrae are nearly identical, the configuration of cervical, dorsal and sacral ribs and their pattern of articulation are similar. In contrast to the condition in *Petrolacosaurus*, the caudal regions of *Prolacerta* and *Youngina* are short

and the laterally directed ribs appear to be firmly fused to the centra. The pelvic girdle is similar to that of *Petrolacosaurus*. The limbs are lightly built, with the distal paired limb elements equal in length or longer than the proximal elements. The tarsus of *Prolacerta* is derived compared to *Petrolacosaurus* in lacking a discrete fifth tarsal bone and in having a hooked fifth metatarsal.

This group appears to have the equivalent position among diapsid reptiles as the eothyridids have had among pelycosaurs (Romer and Price, 1940)—a provisional "garbage bag" assemblage of primitive forms. As it now stands the "Eosuchia" has no taxonomic validity because it cannot be defined in terms of shared derived characters not found in any other group. Until this group is thoroughly reviewed, and proper diagnosis provided, no new forms should be placed within it.

Shared Derived Characters Testing the Hypothesis of Relationship Between *Petrolacosaurus* and *Paleothyris*.

The following characters correspond to characters 1-6 in Fig. 26.

1.—*Loss of contact between the postorbital and supratemporal.* In *Eothyris*, other pelycosaurs, millerosaurs and other early amniotes the postorbital has a long posterior process that extends to the supratemporal. None of the captorhinomorphs, *Petrolacosaurus* or diapsids show this primitive condition, and the loss of contact between these bones is considered derived for captorhinomorphs and diapsids.

2.—*Reduction in the size of the supratemporal bone.* In *Eothyris* and most pelycosaurs, in millerosaurs and even in cotylosaurian "amphibians" the supratemporal is a large sheet of bone wedged between elements of the skull table. In *Paleothyris*, captorhinomorphs, and in *Petrolacosaurus* and other primitive diapsids this bone is modified into a small, slender element generally located in a shallow trough of the parietal bone. This condition is considered derived for captorhinomorphs and diapsids. In carnivorous pelycosaurs the same advanced pattern is seen, but is probably arrived to independently within the synapsids.

3.—*Reduction in size or loss of the tabular bone.* In *Eothyris*, and all other pelycosaurs the tabular bone is a large sheet located on the occiput. In *Paleothyris*, and other protorothyridid captorhinomorphs, in *Petrolacosaurus*, *Youngina* and some other diapsids the tabular bone is greatly reduced in size, a condition considered derived for these forms. In captorhinid captorhinomorphs and in many diapsids the tabular bone is lost.

4.—*Proximal and distal limb elements are elongate and lightly built.* In primitive pelycosaurs (Reisz, in press) the limb elements are relatively thick and massively built. Because the postcranial skeleton of *Eothyris* is unknown, no direct comparison is possible. In both *Paleothyris* and *Petrolacosaurus* the proximal and distal limb elements the shaft is exceedingly slender, usually less than 10 per cent of the length; the extremities of the bones are also reduced in size, with the areas of insertion and origin of muscles important in the power stroke and recovery concentrated near the ends. Although this condition is considered advanced for these forms, the heavy captorhinid captorhinomorphs and the aquatic diapsids appear to have secondarily acquired massive limbs.

5.—*The crus and pes are narrow and long with overlapping metatarsals and metacarpals.* In most pelycosaurs (Romer and Price, 1940) the pes and crus are broad and the metatarsals and metacarpals do not overlap. In both *Paleothyris* and *Petrolacosaurus* as well as most protorothyridid captorhinomorphs and primitive non-aquatic "eosuchian" diapsids, the crus and pes are narrow and thus the proximal heads of the metacarpals and metatarsals overlap extensively. Although this condition is considered derived for the above forms, captorhinid captorhinomorphs appear to have either retained or secondarily developed the primitive condition.

6.—*Presence of a single centrale in the pes.* In most pelycosaurs (Romer and Price, 1940) two centralia pedis are present. In *Paleothyris*, as reconstructed by Carroll (1969), there is a tiny lateral centrale, but the medial centrale has the outline of a peanut. This suggests that the tiny lateral element may have been an artifact and the much larger unusually shaped centrale represents the fusion of the two centrale seen in pelycosaurs. In all other captorhinomorphs, in *Petrolacosaurus* and in diapsids a single large centrale is present, considered to represent the derived condition. In a few advanced carnivorous pelycosaurs the same derived condition has been observed, but this probably represents convergence.

Shared Derived Characters Testing the Hypothesis of Relationship Between *Petrolacosaurus* and *Youngina*

The following characters correspond to characters 7-14 in Fig. 26.

7.—*Presence of superior temporal fenestra.* The most significant departures in *Petrolacosaurus, Youngina* and other "eosuchian" diapsids from the captorhinomorph skull pattern involve the development of fenestrae in the skull roof. The upper and lower temporal fenestrae, typical of diapsid reptiles, have the same position and orientation in *Petrolacosaurus* as in *Youngina*. The lower temporal fenestra is, however, similar to that in *Eothyris*. The derived characters listed in the previous section shared by the unfenestrated *Paleothyris* and the diapsid *Petrolacosaurus* with *Eothyris* as the outgroup suggests that the lower temporal fenestrae in the latter two species developed independently.

8.—*The shape and interrelationship of the circumfenestral bones are modified as a result of diapsidy.* In *Petrolacosaurus* the postorbital is triradiate in outline as in *Youngina*, *Prolacerta* (Camp, 1945; Gow, 1975), *Euparkeria* (Ewer, 1965) and numerous other diapsids. The dorsal ramus of the postorbital is in contact with a small lateral projection of the

parietal. The ventral ramus extends down onto the anterodorsal margin of the jugal and the posterior ramus of the postorbital comes in contact with the squamosal forming the anterior half of the intertemporal bar. In *Prolacerta*, and even in the "eosuchian" derivatives, *Kuhneosaurus* (Robinson, 1962) and *Euparkeria*, where the skulls are known in great detail, specific relationships of the postorbital to surrounding bones are the same as in *Petrolacosaurus*, despite differences in other cranial features. In all four genera, the dorsal ramus of the postorbital sends a small wedge between the parietal and the postfrontal. The anteroventral ramus replaces much of the postfrontal and jugal in forming the posterior margin of the orbit, and extends far down onto the inside surface of the latter element, close to the jugal-ectopterygoid suture.

The lateral portion of each parietal is also modified as a result of fenestration. In captorhinomorphs the contact between the parietal and the postorbital and squamosal is extensive. In *Petrolacosaurus*, as in *Youngina* and all other diapsids, these contacts are greatly reduced and the lateral margin of the parietal is deeply emarginated to form much of the edge of the superior temporal fenestra. In addition, the parietal in *Petrolacosaurus* has a narrow lateral process that forms the anteroventral corner of the upper temporal fenestra, a condition also seen in *Prolacerta*, *Kuhneosaurus* and *Euparkeria*.

In *Prolacerta*, *Euparkeria* and *Kuhneosaurus* a well developed flange of the parietal is directed ventrolaterally, roughly parallel to the direction of the adductor muscle action. The condition in *Youngina*, where the parietal has a very small ventrolateral process, probably represents an intermediate stage between *Petrolacosaurus* and the Triassic diapsid reptiles. A well developed ventrolateral process of the parietal is also seen in modern lizards and *Sphenodon*. It is to the dorsal surface of this flange that much of the adductor musculature is attached. This adaptation represents a secondary stage in the evolution of the

upper temporal fenestra and probably developed in response to the need for more secure muscle attachment. The presence of the temporal opening provided the opportunity of attaching muscle fibers to the outside surface of the parietal. A similar development is seen in advanced mammal-like reptiles, where the adductor musculature also invades the dorsal surface by passing through the lateral temporal opening. This occurs long after initial fenestration and extensive adaptive radiation of early mammal-like reptiles—the pelyeosaurs.

The squamosal of *Petrolacosaurus*, although retaining its plate-like configuration, is modified anteriorly and dorsally to form the margins of the temporal openings and the intertemporal bar. As in *Youngina* and all other diapsids, the contact between the squamosal and the postorbital is much reduced over the condition in captorhinomorphs. The posterior part of the jugal is modified from a plate-like sheet to two relatively narrow bands that extend dorsally and posteriorly. The large suture between the jugal and squamosal of captorhinomorphs is replaced in *Petrolacosaurus* by the lower temporal opening.

9.—*Presence of a well developed suborbital fenestra.* Elongate, well developed suborbital fenestrae are seen in *Petrolacosaurus*, *Youngina* and all other diapsids. No suborbital fenestrae are present in *Paleothyris*, captorhinomorphs or pelyeosaurs.

10.—*The maxilla, palatine, ectopterygoid and jugal bones and their interrelationships are modified as a result of the presence of the suborbital fenestra.* As in *Youngina*, *Heleosaurus* and other diapsids the suture between the cheek (maxilla) and the palate (palatine and ectopterygoid) in *Petrolacosaurus* is interrupted by the suborbital fenestra. The suture between the palatine and maxilla is reduced in length and part of the alveolar shelf of the maxilla is smooth. The ectopterygoid in *Petrolacosaurus* is smaller than in *Paleothyris* and other protorothyridids (Carroll and Baird, 1972) and has a robust lateral projection. The contact between the ecto-

pterygoid and the cheek is greatly reduced, as the jugal develops a small oval medial process for attachment to the lateral process of the ectopterygoid. There is no contact between the ectopterygoid and the maxilla. The same arrangement is found in *Youngina*, *Heleosaurus*, *Euparkeria* and even *Kuhneosaurus*. In *Paleothyris* and other protorothyridids the palato-maxillary suture extends to the posterior end of the palatine. In addition, it is probable that the ectopterygoid also attached suturally to the maxilla, since in these forms the ectopterygoid was a posterior extension of the plate-like palatine (Carroll, 1969). In captorhinids the ectopterygoid is lost, and the maxillary contact with the ectopterygoid is replaced by a strong contact between the jugal and the pterygoid (Heaton, 1979). In advanced pelyeosaurs such as *Dimetrodon*, the jugal also comes to brace the pterygoid, while the ectopterygoid-maxilla suture is reduced.

11.—*A pair of well developed post-temporal fenestrae are bounded in Petrolacosaurus, by a narrow occipital flange of the squamosal, the small tabular, the supraoccipital and the well developed paroccipital process of the opisthotic.* In *Youngina* these fenestrae are somewhat larger than in *Petrolacosaurus*, but are of fundamentally similar configuration. In *Paleothyris* and primitive captorhinomorphs the occiput is poorly known, but the post-temporal fenestra appears to be much smaller than in *Petrolacosaurus* (Carroll, 1969). In pelyeosaurs the post-temporal fenestra is greatly reduced as a result of the plate-like configuration of the tabular and of the supraoccipital-opisthotic complex (Romer and Price, 1940, Fig. 8).

12.—*The relative size of the skull, as indicated by the ratio between the length of the skull and trunk, is considerably smaller in Petrolacosaurus than in Paleothyris and captorhinomorphs, and is similar to that in Youngina and Helcosaurus.* The postorbital region of the skull is much reduced in *Petrolacosaurus* and *Youngina*. The orbits in *Petrolacosaurus*, *Youngina* and other early

diapsids are, on the other hand, relatively larger than in captorhinomorphs.

13.—*The limbs are long.* The humerus and femur in *Petrolacosaurus* are equal in length to about seven mid-dorsal vertebrae. In *Youngina* and *Kenyasaurus* the femora retain the same relative length, but the humeri are relatively shorter, equal in length to about five trunk vertebrae. In *Paleothyris* and most primitive captorhinomorphs the femora and humeri are equal in length to from 4.5 to 5 dorsal vertebrae. In "eosuchians" the radius and ulna, tibia and fibula are nearly equal to (*Youngina Galesphyrus, Kenyasaurus*) or even longer than the humerus and femur respectively (*Prolacerta*). The distal end of the tibia of the above genera is relatively much larger than that of the captorhinomorph *Paleothyris*, suggesting a firmer joint with the astragalus.

14.—*Locked tibio-astragalar joint.* The pes of *Petrolacosaurus* is generally similar to that of *Galesphyrus, Prolacerta, Kenyasaurus,* and *Tangasaurus* (the pes of *Youngina* is poorly known) except for the relatively large size of the proximal elements (Carroll, 1977). The tibial facet of articulation on the astragalus of *Petrolacosaurus*, formed by two longitudinal ridges separated by a deep trough fits snugly onto the distal articular surface of the tibia to form a firm, locked joint. This configuration can be detected only if the tarsus is exposed in ventral or medial views. Thus, only *Petrolacosaurus* and *Kenyasaurus* are now known to have this character, but it is probable that other "eosuchians" have the same pattern. No pelycosaur, millerosaur or captorhinomorph has this advanced condition.

Petrolacosaurus Compared With *Araeoscelis*

The reptile *Araeoscelis* from the Lower Permian of Texas has been often allied by Romer (1956, 1966) and Williston (1925) with a group of poorly known late Permian and early Triassic genera, referred to as protorosaurs. Both Vaughn (1955) and Carroll (1969) felt, however, that *Araeoscelis* and a closely related form, *Kadaliosaurus* from the Lower Permian of Europe, should be placed within the captorhinomorphs on the basis of their similarities to the primitive captorhinomorphs.

Vaughn (1955) has also recognized the possibility that *Araeoscelis* and *Petrolacosaurus* are closely related and suggested that they may belong within the same family. In fact, these genera resemble each other so closely that there is no doubt about their close relationship in spite of some apparently significant differences in their skulls. These two reptiles differ only in a few osteological features.

The dentition in *Araeoscelis* is robust and shows some cusp development in contrast to the delicate, piercing type of dentition seen in *Petrolacosaurus.* In association with this adaptation to a different type of diet, the massive prefrontal extends down to the maxilla and excludes the thin lacrimal from the orbit. The postorbital has a long posterior projection that reaches the supratemporal. A recently uncovered specimen of *Araeoscelis* confirms Vaughn's interpretation of only upper temporal fenestrae in the postorbital portion of the skull roof. The postorbital region of the skull is very deep with the articulation between the jaws far below the level of the maxilla. The occipital plate as restored by Vaughn (1955), is somewhat more extensive than in *Petrolacosaurus* and the post-temporal fenestra are therefore small. This interpretation is based on a single, poorly preserved occiput in an immature specimen. The lower jaw is also relatively massive. All these differences in cranial morphology may be adaptations of *Araeoscelis* to a different diet from the insectivorous *Petrolacosaurus.*

The atlantal centrum in *Araeoscelis* is indistinguishably fused to the axial intercentrum, a condition which is somewhat advanced over that in *Petrolacosaurus.* There are nine elongate cervical vertebrae in *Araeoscelis*, according to Vaughn's reconstruction *versus* six in *Petrolacosaurus.* The neural

arches of the two genera differ in that those of *Araeoscelis* have lower neural spines and the diapophyses and parapophyses are widely separated in the dorsal region of the column, with no bony web to connect them. The girdles are very similar; the only distinguishing features are the wider scapular blade in the pectoral girdle and the ischiadic notch of the pelvis in *Petrolacosaurus*. The limbs in *Araeoscelis* are slightly more specialized than in *Petrolacosaurus* in the presence of a fully enclosed ectepicondylar foramen on the humerus *versus* a supinator process, in having a more slender femur, a cnemial process on the tibia and in occasional fusion of the fourth and fifth tarsals. These few osteological differences in the postcranial skeleton can be readily accounted for by the fact that *Petrolacosaurus* is the larger (therefore requires relatively more bony support) and geologically older animal (therefore more primitive in structure).

Clearly *Petrolacosaurus* and *Araeoscelis* are closely related, with the younger genus specialized to a diet that necessitates a stronger, more massive skull. There are three possible ways of interpreting the morphological characteristics of these two genera: (1) they evolved separately from an unfenestrated ancestor which already achieved some of the posteaptorhinomorph skeletal features shared by both genera; (2) they evolved from a reptile with an upper temporal fenestra, by strengthening the skull in the line leading to *Araeoscelis*, and by lightening the skull and also developing a lower temporal fenestra in the line leading to *Petrolacosaurus*; (3) *Araeoscelis* evolved from a diapsid condition like that of *Petrolacosaurus* by closure of the lower temporal fenestra during adaptation to a different diet.

Similarities in the configuration of the upper temporal fenestra and of the suborbital fenestra suggests that one of the latter two possibilities may be valid. A more precise interpretation of the taxonomic position of *Araeoscelis* and the evolutionary relations of the two genera must await the results of a study (now in progress) of two recently discovered and well preserved skeletons of *Araeoscelis*.

HEARING IN *PETROLACOSAURUS* AND
OTHER EARLY REPTILES

Advanced cranial osteological features of late Permian and early Triassic "eosuchians" include modifications of the posterior margin of the cheek, the stapes and the posterior end of the mandible. The posterior border of the squamosal in *Youngina* does not completely cover the dorsal process of the quadrate, so that this bone is visible in lateral view. The posterior border is slightly concave. The shaft of the stapes is slimmer than in captorhinomorphs and *Petrolacosaurus*. This arrangement of a light stapes and a slightly concave quadrate is somewhat similar to that seen in modern lacertilians, where the strongly notched quadrate supports a tympanic membrane. It has therefore been assumed that *Youngina* had a tympanum. The condition in *Euparkeria* and *Prolacerta* is even closer to that seen in living lizards. The concavity of the posterior edge of the quadrate is much stronger than in *Youngina*, there is a well developed retroarticular process and the stapes is reduced to a slender rod.

In *Petrolacosaurus*, on the other hand, the squamosal forms the slightly convex posterior border of the skull and the dorsal process of the quadrate is completely covered. The stapes is massive (Figs. 5 and 13).

Consideration of the functional implications of structures observed in early reptiles is impossible without comparisons with living forms. Although generalizations about the middle ears in living reptiles are tenuous because of the morphological differences seen, even within families, certain overall characteristics can be noted in forms which are sensitive to airborne sound. Reptiles sensitive to airborne sound have a well-developed tympanum held taut by extensive bony support. The areal ratio between the tympanum and stapedial footplate is large (at least 30 to 1) and the mass of the stapes is low. The stapes is typically a slender osseous rod with a slightly expanded footplate that is suspended

within the oval window (Werner and Wever, 1972).

In lizards the quadrate, freed from its squamosal cover, forms the strongly notched posterior border of the cheek. In addition, the lower jaw extends backward, beyond the articulation between the quadrate and articular. In most extant lizards the strongly notched quadrate and the retroarticular process of the lower jaw support a large tympanic membrane. The posterior border of the tympanum is in part supported by the M. depressor mandibularis which originates from the top of the occipital plate of the skull and inserts on the posterior end of the retroarticular process. Because similar osteological features are seen in such Triassic diapsids as *Prolacerta, Euparkeria, Kuhneosaurus, Paleogama* and *Paliguana*, it is possible that in these forms the quadrate and the retroarticular process supported a relatively large tympanum. None of these structural features are, however, seen in *Petrolacosaurus*, captorhinomorphs or even pelycosaurs. There is neither a notch at the posterior edge of the cheek, nor a posteriorly directed retroarticular process. Under these conditions, the M. depressor mandibularis had to hug the posterior border of the skull as it extended down to the lower jaw. There was therefore, no place for the tympanum. There is no evidence for any bony support for a tympanum. This support would be needed to maintain high membrane elasticity in the hydraulic and curved-membrane level action of the middle ear mechanism (Wever and Werner, 1970; Manley, 1972).

All these features indicate that there could be no tympanum in *Petrolacosaurus*, captorhinomorphs or pelycosaurs. Vaughn (1955), Hotton (1959) and Parrington (1955) have suggested that the tympanum in primitive reptiles were located more medially and were connected to the outside by an external audi-

tory meatus. These reconstructions did not take into account that the tympanum had to be located at the distal end of the stapes and that the suggested locations of the tympanum were occupied by extensive cranial and neck musculature.

In captorhinomorphs, pelycosaurs and *Petrolacosaurus* the stapes is very massive and is firmly attached both to the quadrate and the braincase. Its higher inertia makes initiation of movement much more difficult than in modern forms. The footplate of the stapes is also very large. This makes high areal ratios between a tympanic membrane and stapedial footplate impossible. To achieve comparable areal ratios to those seen in modern reptiles, the tympanum would have to be too large to fit anywhere behind the skull. It is even more significant that the large footplate was fitted within a bony socket of the braincase, the fenestra ovalis externa (Heaton, 1979), and that the distal end of the stapes was probably continued in a short cartilaginous process that fitted in the stapedial recess of the quadrate. All of this indicates that the stapes could not form an effective link within a mechanical transducer system sensitive to airborne sounds. Although Hotton attempted to show that the massive stapes of *Dimetrodon* can be activated by a relatively small membrane, his poorly calibrated experiments (1959, Fig. 1B) provide no useful evidence in this regard. No attempt was made during the experiments to establish the intensity of airborne sound. In addition, the model was not intended to approach the structural pattern of the middle ear of any reptile.

The middle ear in captorhinomorphs, pelycosaurs and *Petrolacosaurus* could not function as in most modern reptiles. In modern reptiles a highly effective mechanical transducer amplifies small sound pressures impinging upon a large tympanic membrane into strong pressures exerted at the fenestra ovalis. Without an effective transducer mechanism the great difference in impedances of air and inner ear could not be compensated,

and most of the aerial sound impinging upon the inner ear through various pathways would not be transmitted, but absorbed and reflected (Wever and Lawrence, 1954). We would, therefore, expect the ear of these primitive reptiles to be insensitive to airborne sound.

In spite of the supposed relative insensitivity of the primitive reptilian type of ear to airborne sound, there is little doubt that with reduction of stapes mass and the development of bony support for a tympanum, the ability of the ear to perceive low frequency airborne sounds would greatly increase. The presence in *Euparkeria* and *Prolacerta* of a light stapes and a large area for a bone supported tympanum, suggests that these genera have already achieved higher sensitivity to airborne sounds than captorhinomorphs, or *Petrolacosaurus*.

It is relatively easy to derive the structural condition of the ear region of *Prolacerta* and *Euparkeria* from that in captorhinomorphs or *Petrolacosaurus*. The lightening of the stapes, the loss of the squamosal cover of the posterior end of the quadrate and the associated notching in the quadrate are related with the middle ear's increasing efficiency as a mechanical transducer. The development of a retroarticular process may, however, have the dual advantage of (a) increasing the mechanical advantage of the M. depressor mandibularis, and (b) increasing the efficiency of the middle ear by both increasing the available surface area between the quadrate and the M. depressor mandibularis, and by providing better support for the ventral part of the tympanum. What conditions would lead to selection of a middle ear sensitive to airborne sound? Vocal communication has been cited as a possible factor (Manley, 1973). The fossil evidence indicates that middle ears with efficient transducer mechanisms developed from the captorhinomorph condition at least three times (therapsids, "eosuchians" and chelonians).

Studies now in progress (Heaton, pers. comm.) indicate that the stapes in primitive

reptiles braced the braincase against the quadrate in a metakinetic skull. In the lineage giving rise to lizards anterior rotation of the braincase relative to the skull roof (metakinesis) was limited by the development of accessory structures on the supraoccipital and parietal and, to a lesser extent, by the full ossification of the paroccipital process, thereby freeing the stapes from its supportive function. Once freed, the stapes become a hearing ossicle. The condition seen in *Petrolacosaurus* may represent the first stage in the sequence, where the stapes is still massive, but in contrast to the condition seen in primitive captorhinomorphs, the paroccipital process is fully ossified and extends far laterally. *Youngina* would represent an intermediate stage, where several modifications of the ear region are taking place. The type specimen of *Youngina capensis* shows that the squamosal no longer covers the posterior margin of the quadrate, and the posterior margin of the quadrate is slightly concave, but not notched. The type of *Youngopsis rubidgei* has a stapes with a relatively slender shaft and the paroccipital process extends dorsolaterally to a notch between the squamosal and the quadrate. Both *Youngina* and *Heleosaurus* have very short retroarticular processes. It is unlikely, however, that a tympanum was present in these "eosuchians." The condition seen in *Prolacerta*, *Palacagama* and *Euparkeria* represent the final stages in this sequence, where the osteological modifications necessary for having a middle ear sensitive to airborne sound have been completed.

CONCLUSIONS

The detailed study of the osteology of the Pennsylvanian reptile *Petrolacosaurus kansensis* adds to our understanding of the anatomy of early reptiles. A good knowledge of the osteology of this form also permits detailed comparisons with other Paleozoic reptiles.

Several authors have suggested that *Petrolacosaurus* should be allied with pelycosaurs. This association is invalid for the following reasons: As already indicated, the morphological features in which this reptile is derived (the synapomorphies of Hennig) over the captorhinomorph pattern are not at all similar to the derived features seen in pelycosaurs. The similarities between *Petrolacosaurus* and early pelycosaurs are mostly primitive characters, also shared with the captorhinomorphs. In addition it has been argued (Reisz, 1972) that the lower temporal opening seen in the pelycosaurs developed in response to selection for more efficient use of the jaw musculature in forms of increasing body size. The skulls of the Middle and Upper Pennsylvanian pelycosaurs are larger and considerably more massive than the skulls of either *Petrolacosaurus* or early captorhinomorphs. Early pelycosaurs were, therefore, able to include into their food supply animals of greater size, and were probably able to feed upon captorhinomorphs and other small contemporary tetrapods. In the postcranial skeleton, pelycosaurs show advances over the primitive captorhinomorph pattern that can be readily attributed to accommodation for the greater body size. *Petrolacosaurus*, on the other hand, evolved in a completely different direction. Its diapsid skull configuration probably developed in response to the selective advantage of maintaining a relatively small, light-weight skull at the end of a long neck. The postcranial features indicate that *Petrolacosaurus* was more agile than the captorhinomorphs or pelycosaurs. The combination of a relatively small, lightly-built skull and

greater agility suggest that this reptile adapted to a somewhat different food supply than captorhinomorphs and pelycosaurs. It is difficult to specify what food was selected, but it is probable that *Petrolacosaurus* fed mainly on terrestrial arthropod invertebrates.

Close phylogenetic relationships of *Petrolacosaurus* to early "eosuchians" are indicated by derived characters in common with *Youngina, Galesphyrus, Heleosaurus, Kenyasaurus*, and *Prolacerta*. Most derived petrolacosaurid features, not seen in either captorhinomorphs or pelycosaurs, are found in *Youngina*. The similar pattern of fenestration in the skulls of *Petrolacosaurus* and *Youngina* is the most significant of these advanced features. *Youngina* and other diapsids are more advanced than *Petrolacosaurus* in some cranial features, but the latter genus is geologically much older, and understandably more primitive. The most significant of these specialized features, not found in *Petrolacosaurus*, involve osteological modifications towards development of a middle ear system sensitive to airborne sound. There is evidence to indicate that such modifications in the region of the ear may have been initiated by the adaptations already seen in *Petrolacosaurus*. Similarities in function, shape and orientation of the temporal openings and the interrelationship of the circumfenestral bones are strong indications that the upper and lower temporal fenestrae in *Petrolacosaurus, Youngina* and other diapsids are phylogenetically related.

The erection of the family Petrolacosauridae by Peabody (1952) is valid because there are several derived characters that can be used to define this taxon. These derived characters are: an unusually slender, lightly built premaxilla, unusually thin walled marginal dentition, six elongate cervical vertebrae, mammillary processes on the neural arch of the first sacral vertebra, a well developed ischiadic notch and forelimbs equal in length

to hindlimbs. Placement of the family Petrolacosauridae at the base of the order "Eosuchia" (Peabody, 1952; Reisz, 1977) is however inappropriate because the latter taxon is undefined. The inclusion of early diapsid reptiles into the order "Eosuchia" solely on the basis of characters that are primitive for diapsids is invalid. Both the best known "eosuchian" family, the Younginidae and the order "Eosuchia" therefore need to be reviewed and testable hypotheses of relationships constructed before their phylogenies can be reevaluated.

Acceptance of *Petrolacosaurus* as the oldest known diapsid reptile indicates a long hiatus in the fossil record of the diapsid radiation between its first evidence in the late Pennsylvanian and the subsequent differentiation in the late Permian. The extent of the early Triassic diapsid radiation confirms that the origin of the group should be sought much earlier, probably well within the Paleozoic, as *Petrolacosaurus* appears to substantiate, but the intervening gap is puzzling.

The conditions of preservation and the nature of the fossils at Garnett, Kansas suggest that *Petrolacosaurus* and other terrestrial tetrapods, invertebrates and plants were washed into a quiet lagoon from dry ground (Peabody, 1952). The gap in the fossil record may indicate that the early diapsids lived in environmental conditions which were not, under normal conditions, conductive to preservation—areas away from standing water, or that areas where they may have been buried have either been eroded away or not exposed by erosion.

Recent studies of Upper Permian and Lower Triassic diapsid reptiles from South Africa (Carroll, 1975, 1976, 1977; Gow, 1975; Harris and Carroll, 1977) and a preliminary examination of Permo-Triassic diapsids from Madagascar and Tanzania, show that this stage of the diapsid evolution is far more complicated and extensive than formerly believed. A more complete picture of the early diapsid adaptive radiation is required in order to understand fully how *Petrolacosaurus* relates to later diapsids.

SUMMARY

Fossil evidence indicates that *Petrolacosaurus kansensis*, a primitive diapsid reptile from the Upper Pennsylvanian of Garnett, Kansas presents a combination of morphological features that place it near the base of subsequent diapsid lineages, while also evidencing close relationships to captorhinomorph reptiles. Shared derived characters (synapomorphies) of diapsids and *Petrolacosaurus* include the presence of well developed superior and inferior temporal, occipital and suborbital fenestrae. Close phylogenetic relations between *Petrolacosaurus* and protorothyridid captorhinomorph reptiles is indicated by the following shared derived characters: the supratemporal is reduced to a small narrow sliver of bone that lies in a shallow groove formed by the parietal and squamosal, the postorbital does not reach the supratemporal, the tabular is small, and the limbs are lightly built. Comparison of this species with captorhinomorphs and other early reptiles indicates that the diapsid skull configuration may have developed in response to the selective advantage of maintaining a relatively small, light weight skull at the end of a long neck. The configuration of the ear region in both primitive captorhinomorphs and *Petrolacosaurus* indicates that these animals were insensitive to airborne sounds. There is, however, evidence to suggest that the selective forces for modifications towards development of a middle ear system sensitive to airborne sounds may have been initiated in *Petrolacosaurus*.

Petrolacosaurus is the only described member of a distinct family of diapsid reptiles whose exact position is difficult to ascertain until the younger diapsids, commonly called the "eosuchians," become better known.

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